PROCEEDINGS OF
THE LINNEAN SOCIETY OF LONDON

Session 1949–50

Vol. 162 Part 1

PROCEEDINGS OF THE GENERAL MEETING ON 13 October 1949

Professor F. E. Fritsch, F.R.S., President,
in the Chair.

The Proceedings of the Anniversary Meeting held on Tuesday, 24 May 1949, having been circulated, were taken as read and confirmed.

Professor F. E. Weiss, F.R.S., welcomed the new President, and on behalf of the Fellows expressed their good wishes for his Presidency of the Society. The President, in reply, thanked Professor Weiss and the Fellows for the honour done him and promised to use his best endeavours to further the interests of the Society.

The President read for the first time the following proposed alteration in the Bye-Laws,—

That Bye-Laws, Chap, 1, Sect. 1, shall read :—

> ' Sect. 1. The number of Fellows shall be limited to one thousand, exclusive of Honorary Members, Foreign Members and Associates. The method of election shall be by Ballot '.

The President read a letter from Mr. William Stone, M.A., F.L.S., thanking the Society for its congratulations on his seventieth year of Fellowship.

The following were thanked for gifts made to the Library since the last Meeting :—Dr. Nazir Ahmad, Mr. Eric W. Baxter, Mr. A. E. Blake, K.L.B., Mr. H. H. Bloomer, British Museum (Natural History), Mr. W. G. Burton, Professor G. D. Hale Carpenter, M.B.E. The Right Hon. The Earl of Cranbrook, Dr. David Fairchild, Mr. J. E. Hamilton, Mr. M. R. Henderson, Mr. R. E. Holttum, Trustees of the Imperial Botanical Conference, 1935, Prof. R. C. McLean, Mr. Richard Morse, Mr. S. D. Onabamiro, Mr. Christopher A. W. Sandeman, Dr. F. M. L. Sheffield, Mrs. C. M. Snow, Dr. C. G. G. J. van Steenis, Col. F. C. Stern, O.B.E., M.C., Mr. G. E. Trease, Mr. J. H. Turner, Capt. F. Kingdon Ward, Professor F. E. Weiss, F.R.S., and the Exors. of the late Dr. L. Richmond Wheeler.

The following Fellows signed the Obligation in the Roll and Charter Book, and were Admitted Fellows :—Professor Francis William Rogers Brambell, D.Sc., F.R.S., Mr. Douglas Maxwell Bryce, B.Pharm., Mr. Edward Cowper Green, B.A., Mr. Ronald Herbert Hall, Mrs. Una Christina Mason, M.Sc., The Right Hon. The Earl of Morton, M.A., Mr. Ronald Purdy, B.Sc., Dr. Redcliffe Nathan Salaman, J.P., M.A., M.D., F.R.S., Mr. Christopher Albert Walter Sandeman, Mr. George Reginald Allen Short, Ph.C., Mr. Geoffrey Brian Boyd Thomas, B.Sc., Mr. Ernest Alfred Walters and Mr. Leslie Francis Seawell Ward, M.A.

Recommendations for election to Associateship were read for the first time :—*Honoris causa ;* Harry Britten. *Ordinary* : Basil Walston Ribbons, B.Sc., Gerald Haig Mickleburgh.

The President reported the following deaths :—Miss G. Lister, Mr. Albert Wilson, Sir Frederick W. Moore, Mr. D. J. Scourfield, I.S.O., and Colonel G. H. Evans, C.I.E., C.B.E., Fellows of the Society ; Prof. P. Marchal, Prof. A. Rehder and Prof. F. Silvestri, Foreign Members.

The following communications were read and discussed,—

Prof. H. BURTON. Stem of a lupin showing proliferation. (Exhibit.)

Mr. S. SAVAGE. Abnormal growth in the flowering stem of the foxglove. (Exhibit.)

(Dr. B. Barnes gave an account of these two exhibits ; the President added some remarks.)

Prof. G. E. HUTCHINSON. The guano islands ecologically, climatically and palaeogeographically considered. (Discussed by Lt.-Col. R. B. Seymour Sewell, C.I.E., F.R.S., Dr. Redcliffe N. Salaman, F.R.S., and the President ; Prof. Hutchinson replied.)

Abstract,—

Prior to total exploitation in the mid-19th century, the principal guano islands of the Peruvian coast bore deposits of consolidated bird-droppings up to about 50 metres in thickness. The archaeological evidence assembled by Professor G. A. Kubler and the stratigraphic evidence brought together by the speaker indicate that this huge accumulation could have formed in a few thousand years. Prior to initiation of deposition on the Peruvian coast there was certainly much guano being laid down on the coast of Chile, but farther north where the main deposits are formed to-day it is probable that the prevailing climatic regime was that of modern ' abnormal ' wet years. In the central Pacific phosphatic guano deposits of post-glacial date and of large size, exceeding 10,000 tons, are confined to the area of low rainfall along the equator, within the zone of the South-East trade-winds and in the neighbourhood of the equatorial divergence. There is, however, reason to suppose that in such a region deposits of the size implied by the phosphate beds of Nauru, Ocean Island and some other localities in the Pacific, Christmas Island in the Indian Ocean and some West Indian Islands, could not have formed in a reasonable time. It is suggested that some huge deposits originated in periods of greatly enhanced oceanic fertility, due to a lowering of the vertical stability of the oceans when the supply of cold water was reduced during interglacials.

Prof. J. REICHERT. A revision of the plant-geographical term ' element'. Amendments and proposals. (Discussed by Dr. W. B. Turrill, Mr. I. H. Burkill, Dr. J. Ramsbottom, O.B.E. ; Prof. Reichert replied.)

Abstract,—

The method used in plant-geographical analysis of a certain floristic area is the division of the plants in distributional units called ' elements '. The term ' element ' which was first introduced by H. Christ (1867) was subject to a large measure of conflicting interpretations. To mention only the misuse of the term ' pontic element ' originally applied by Kerner (1887) in a geographical sense, to designate the area of plants extending from the shores of the Black Sea to the Alps and Carpathians. This designation was used by subsequent investigators in an entirely different context, i.e. in a vegetational (steppe) ecological (heliophile), migratory (route) and in a historico-genetical respect (origin).

The reason for these contradictions lies in the natural development of botanical science implying new plant-geographical approaches. The various authors include in the old singly existing term ' element ' a variety of new plant-geographical aspects. The only suitable method of contending with these difficulties is to form adequate terms for each specialized aspect.

In 1921 (*Engler's Bot. Jahrb.* **5** : 598) Reichert suggested the use of the term ' component ' for the designation of recent distribution, the term ' migrant ' for migration of plants. He also desired to retain the old term ' element ' for origin characterization in the sense of Engler (1878). In 1940 (*Pal. Journ. of Bot., R.S.*, **3** : 183) Reichert proposed to revive the old name ' type ' of Watson (1835) used by him for ecological description of plants for the same purpose. New proposals are now put forward for the characterization of a geographical natural area.

Discussion,—

Dr. W. B. TURRILL commented upon the speaker's reference to J. D. Hooker's confused use of the term ' element '. He said that so much of Hooker's work was of a pioneer nature that it was to be expected that further research would necessitate clearer definition and restriction of some of his terms. A different example of this is the term ' parasites ' which Hooker, in the *Himalayan Journals*, uses to include what we should now distinguish as ' epiphytes '. Dr. Turrill agreed with Prof. Reichert that the various concepts outlined in the paper should be carefully distinguished but he doubted the necessity of the terminology proposed. If terms were essential, he considered it might be better to start afresh and manufacture new terms that could be used internationally. Some, at least, of the English terms suggested had had so many meanings attached to them that they were almost certain to remain ambiguous in general usage. The possible use of new terms in Latin was suggested. The use of the word ' type ', as proposed by Prof. Reichert, was open to strong objections because it already had a precise application in taxonomy.

Mr. I. H. BURKILL commented, using *Dioscorea balcanica* by way of illustration, that ' component ' is undoubtedly its appellation when speaking of the Balkan Flora and ' element ' is its also, in reference to the fact that it is endemic, ' element ' but not ' component ' contrasting with ' migrant ' ; and that he would consider himself correct in calling it ' type ' in such a connotation as Himalayan type, its closest allies being in stronger force there, but in applying the word ' type ' thus, he would take precautions for being understood.

PROCEEDINGS OF THE GENERAL MEETING ON 27 October 1949

Professor F. E. FRITSCH, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 13 October 1949, having been circulated, were taken as read and confirmed.

The President read for the second time the proposed alteration in the Bye-Laws, Chap. 1, Sect. 1.

The following were thanked for gifts made to the Library since the last Meeting :—Professor G. D. Hale Carpenter, M.B.E., Mr. Richard Morse, Dr. Redcliffe N. Salaman, F.R.S., Mr. F. C. Sawyer and Professor James Small.

The following Fellows signed the Obligation in the Roll and Charter Book, and were admitted Fellows :—Dr. Robert Churchill Blackie, Mr. Peter S. Green, B.Sc., Dr. Leonard William Poel, B.Sc., Mr. Oleg Vladimir Polunin, M.A., and Mrs. Cecil Ivry Sandwith.

The President reported the following death :—Miss Ida Margaret Hayward, Fellow of the Society.

Candidates for Associateship were balloted for and elected :—As an Associate *honoris causa*, Harry Britten ; as ordinary Associates, Basil Walston Ribbons, B.Sc. and Gerald Haig Mickleburgh.

The following communications were read and discussed :—

Dr. R. F. Lawrence. Lantern-slides illustrating the habits of the South African Peripatus. (Discussed by Dr. S. M. Manton, F.R.S., and the President.)

Discussion on Heteroecism, opened by Dr. Malcolm Wilson and Dr. Edward Hindle, F.R.S.

Mr. Malcolm Wilson. The origin of heteroecism in the Uredinales.

Dr. Edward Hindle, F.R.S. Heteroecism in animals.

(A general discussion followed, in which the President, Dr. J. Ramsbottom, O.B.E., Dr. C. F. A. Pantin, F.R.S., Prof. G. D. Hale Carpenter, M.B.E., Dr. P. D. Critopoulos, Mr. Robertson and Miss E. M. Blackwell took part ; Dr. Hindle and Dr. Wilson replied.)

DISCUSSION ON HETEROECISM

THE ORIGIN OF HETEROECISM IN THE UREDINALES

By Dr. Malcolm Wilson.

The origin of heteroecism of the Uredinales is closely bound up with the phylogeny of the group. Following the views of de Bary, it is suggested that the Uredinales were derived from an ascomycetous fungus at a period prior to the appearance of the Angiosperms. This fungus, which existed as a parasite on some Gymnosperm, possessed spermogonia and perithecia ; as the result of a mutation the cells of its ascogenous hyphae, failing to produce asci, separated and formed binucleate spores. The perithecium was thus transformed into the aecidium. The aecidiospores, as in the present-day rusts, were unable to infect the Gymnosperm host ; they were numerous and were widely distributed and, as the exploitation of a purely accidental compatibility which happened to exist without any process of gradual establishment, some of these spores were able to infect certain mosses and ferns upon which they fell. The binucleate mycelium developed in the fern produced repeating spores (uredospores) and ultimately teleutospores in which the conjugate nuclei fused ; on germination the simple primitive basidium characteristic of the rust was produced and formed uninucleate basidiospores which infected the Gymnosperm host.

In addition, from the diplont on the fern different types of organisms arose : (1) Parasites on ferns resembling forms now placed in the Auriculariales ; (2) Autoecious rusts producing basidia only, resembling existent species on various primitive Angiosperm hosts; (3) Parasites of scale insects producing uredospores and teleutospores resembling those of *Uredinella* species; (4) By adoption of the saprophytic habit, forms leading to the higher Basidiomycetes.

There is no evidence that the diplont formed on mosses brought about infection of the Gymnosperm host. It gave rise to forms resembling species of *Eocronartium* and *Iola* and possibly to autoecious rusts resembling *Goplana* sp.

HETEROECISM IN ANIMALS

By Dr. Edward Hindle, F.R.S.

The adaptation of animals to a parasitic mode of life occurs in almost every Phylum of the Animal Kingdom, and has resulted in the evolution of a bewildering variety of organisms presenting a very wide range of morphological and physiological modifications. It is obviously one of the most successful methods of ensuring a food supply—at least during the life time of the host—and also affords protection against desiccation, an almost equally important factor in desert regions, where as a result one generally finds a high degree of parasitism.

In many respects parasites resemble island faunas in being isolated from competition with other species, apart from any other parasites that may invade the same individual host. Since it is rare to find any animal with an alimentary canal or circulatory system completely free from parasites, it will be obvious there are good reasons for believing that the number of species adopting this parasitic mode of life must far exceed that of all free-living animals.

There seems little doubt that parasitism must have existed from the earliest times for even in the Palaeozoic Era fossil crinoids have been found carrying parasitic gastropods very similar to those of the present day. Unfortunately, the great majority of parasites are of such a nature that they are not likely to be preserved as fossils and so the affinities of some of the predominantly parasitic groups, such as the Nematodes, present a very difficult problem.

The absence of definite evidence, however, gives more scope for speculative theories, and this evening I am opening a discussion on one very extraordinary habit which has developed in many groups of parasites, that of being dependent on more than one species of host for the completion of the life-cycle.

The adoption of a parasitic mode of life has certain definite limitations, one of which is the difficulty of reaching a new host, and it is in this direction we may look for the origin of heteroecism. In this connexion, there is one outstanding characteristic of parasites, distinguishing them from all free-living forms, that is their power of resisting the defence mechanism of the host. This is a somewhat elastic property for under certain conditions the parasite may be destroyed by its host, but in most cases a kind of balance becomes established and the parasite is able to persist within its host at a certain level of intensity, depending on a variety of factors. This physiological property of resistance to the defence mechanism of the host is carried to extreme in the case of such a parasite as *Leishmania*, which actually invades the clasmatocytes and other cells of the reticulo-endothelial system. One can surmise, therefore, that parasites in general, might be expected to be more likely to be capable of withstanding the defence mechanisms of other species of animals (or plants) in addition to those of their primary host.

I will now consider a few examples, starting with the evolution of some of the blood parasites found in nearly all vertebrates, and with one or two exceptions, transmitted by means of blood-sucking invertebrates.

The first example I have selected is *Rickettsia*, a micro-organism of somewhat doubtful affinities, many species of which live inside the alimentary canal of insects, especially those which feed on blood. The human body-louse, *P. humanus* var. *corporis*, acts as the intermediate host of three or more species of pathogenic *Rickettsiae*, the responsible agents for such diseases as typhus, trench fever, scrub typhus, etc., and in addition its gut may contain a saprophytic species which closely resembles the pathogenic forms, but differs from them in not being able to survive in the human body. But when one considers that a body-louse is living at a temperature approximately that of its human host, and that the *Rickettsia* in the louse has already become a tissue parasite, and is being brought into contact with human blood every time the louse feeds, it does not seem a very big step for a variety to be produced capable of living in human tissues. The habits of lice also favour the introduction of any micro-organism into its human host, for when feeding they commonly pass out faeces which may contain *Rickettsiae*. These infected faeces on the surface of the skin may easily be rubbed into the open wound caused by the bite of the louse, and thus any *Rickettsiae* that may be present have frequent opportunities of invading human tissues. It may be mentioned that in the case of typhus, the causative organism, *Rickettsia prowazeki*, is carried from one person to another by means of the body-louse, but the micro-organism gains entrance to its human host only by this contaminative method.

The blood spirochaetes present a very similar picture. They are responsible for a variety of human relapsing fevers, and are transmitted either by lice or by ticks. Again the method of infection is often contaminative, the bites alone of lice infected with *S. recurrentis* being innocuous. Infected ticks show further stages of evolution, and whilst in some cases the contaminative method of infection persists, in others the spirochaetes are present in the salivary secretion and directly inoculated into the vertebrate host when the tick feeds. In addition spirochaetes may be transmitted hereditarily to the offspring of infected ticks.

The evolution of parasitism in flagellates also seems to have followed a similar course to that outlined above. Again we find that many species of insects, both blood-sucking and non-blood-sucking, contain flagellates, usually inhabiting the alimentary tract and transmitted from one insect to another by means of encysted forms which pass out in the faeces. But some species of flagellates have acquired the property of being able to live in the blood and tissues of animals, or in the latex of certain plants. Among the best known examples are the mammalian trypanosomes and *Leishmania*, both of which are usually transmitted by blood-sucking insects. *Leishmania*, transmitted by sand-flies (*Phlebotomus*), shows a further stage in the evolution of parasitism in its vertebrate host, having invaded its cellular defence system and become intra-cellular, losing its flagellum in the process. It is of interest to consider the behaviour of the non-flagellate stage of *Leishmania* when ingested by *Phlebotomus*. By means of artificial feeding it is possible to induce any species of sand-fly to ingest emulsions of this stage of *Leishmania*. Working with a Chinese strain of *Leishmania donovani*, I found that it developed to the flagellate stage equally well in the crop of three species of sand-flies, including one which normally feeds on lizards and other reptiles, but never on man. All three species, therefore, might be considered potential secondary hosts, but in only one species does a further development take place involving attachment of the flagellates to the anterior wall of the crop and their subsequent invasion of the buccal cavity and proboscis.

Trypanosomes show all stages from cases in which the intermediate host retains the contaminative method of infection, up to such examples as the method of transmission of human sleeping sickness (*T. gambiense*), where the trypanosomes undergo a cyclical development in the gut and then travel to the salivary glands of the tsetse-fly, *Glossina palpalis*, and are inoculated into a new vertebrate host when it feeds.

Turning now for a few minutes to larger parasites, let us consider the Cestodes. These are of special interest since they are all exclusively parasitic and have become profoundly modified in adaptation to this strictly parasitic mode of life. They present various stages in evolution from monogenetic to digenetic species, and may be grouped as follows :—

(1) Some species (e.g. *Hymenolepis nana*) are monogenetic, and complete their life cycle in one host.

(2) Other species, although capable of completing their life cycle in one host, have a facultative intermediate host, usually an insect (procercoid in rat flea, etc.) and thus may be either monogenetic or digenetic (e.g. *Hymenolepis* sp.).

(3) The next stage includes the best known Cestodes (e.g. *Taenia saginata*) typically digenetic species, in which an intermediate host (usually another vertebrate) is essential, but without a ' resting host '.

(4) A further stage comprises digenetic forms in which an intermediate host is essential, but in addition there is a facultative resting host (e.g. Tapeworms of fishes and reptiles). The intermediate host is usually an aquatic insect or crustacean which swallows the eggs. Development takes place in the intermediate host, but if this is swallowed by a species other than the primary host it may remain dormant and can only complete development if ingested by its primary host.

(5) The most advanced stage is found in such an example as *Diphyllobothrium latum*, the broad tapeworm, which inhabits the intestine of man, and also (experimentally) of dogs and cats. The eggs are passed out with the faeces, in very large numbers. They give rise to ciliated embryos (' coracidia ') which must be eaten by certain copepods (e.g. *Diaptomus* sp., in U.S.A.) in order to develop. The coracidium develops into an ' onchosphere ' and then into a ' procercoid ' stage in the haemocoele of the copepod. It cannot develop any further unless it is swallowed by a fish, when it travels first to the liver and then to the muscles, where it becomes an elongated ' pleurocercoid ' larva. If this larva is swallowed by another fish it can survive in the muscles of its new host but can only complete its development to the adult form if swallowed by man, dog or cat.

In the case of *Dibothriocephalus* there seems to be a close relation between the parasite and the first intermediate host as well as its primary host, but this is somewhat unusual. The cysticercus stage of the tapeworms of carnivorous mammals can develop in a wide range of herbivorous animals, though generally it is found in those species which are the natural prey of the particular carnivores concerned.

A somewhat similar example is found in the Trematode, *Clonorchis sinensis*, an important human parasite in the Far East. The adults inhabit the human bile ducts and the eggs pass out with the faeces ; miracidia hatch out from these eggs if they are swallowed by certain water snails. In the snail the miracidium develops into a rounded sporocyst which produces rediae. These develop into cercariae, tadpole-like bodies with long tails which emerge from the snail, attack fishes and encyst in their flesh. If this encysted stage is swallowed by man, e.g. in uncooked fish, the life cycle may be completed.

Although I have only been able to consider these few examples, it is possible in many parasitic groups to find all stages from parasites with only one species of host, through those which have facultative intermediate hosts, to others with obligatory intermediate hosts, and finally to such complex cycles as those found in *Dibothriocephalus* and *Clonorchis*. The governing factor in each case seems to be the difficulty of reaching a new host and of course only those parasites which have solved the problem have survived.

With reference to the origin of heteroecism, there are obvious advantages to a parasite in being able to complete its life cycle in more than one species of host, and in some cases it is difficult to see how a parasite could ever get back to its primary host except in this way. Carnivores, for example, are rarely cannibals, and their feeding habits are such that their food is unlikely to be contaminated with the faeces of their own species. But these faeces containing the eggs or proglottides of tapeworms contaminate pastures, etc., and are very liable to be swallowed by herbivorous animals. If the embryonic cestode were capable of resisting the defence mechanism of its new host it might find favourable conditions for partial growth and thus acquire a secondary host. One could surmise that as development proceeded its antigenic properties would gradually excite a stronger defence reaction on the part of the tissues of its new host, resulting eventually in growth being slowed down and the production of a resting cyst. Only those cysts produced in animals likely to be eaten by the primary host would have any chance of completing their development. If swallowed by the primary host the parasite would once again be in surroundings in which its antigenic properties would not excite the full defence mechanism of its host, and consequently further development would be able to continue. On the other hand, if, as in the case of the pleurocercoid larvae of *Dibothriocephalus* in fishes, the parasite is swallowed by another fish, further development does not take place although it is able to survive. Again only when it reaches the primary host—man, dog or cat—does it find conditions suitable for development to the adult stage.

Discussion,—

Dr. C. F. A. Pantin asked whether there was any evidence in plants or animals that parasites produced an immunity reaction against themselves in their hosts ; and, if so, whether heteroecism would confer an advantage on a parasite by enabling it to overcome such an immunity barrier after passage through a host of a different kind.

Professor G. D. Hale Carpenter alluded to the well-known possibility that flagellate inhabitants of the gut of such insects as house-flies might have become blood-parasites through the fly's habit of feeding from the juices of a sore or wound. It was a common procedure for a fly to regurgitate droplets of fluid and suck them up again, plus dissolved substances. If a regurgitated drop contained gut-flagellates they might become acclimatized to the new medium of vertebrate fluids and thus eventually establish themselves in the blood stream.

Miss E. M. Blackwell spoke in criticism of the assumption that the spermatium functions, or ever functioned, as a sperm fertilizing the aecidium initial ; and drew attention to the many and various hyphal fusions and nuclear migrations which take place in the haploid mycelia within the host tissues.

The President said he did not feel that the two speakers had established any marked degree of contact with one another. Speaking as an outsider, he did not see any difficulties in understanding the heteroecism of animal parasites which, as Dr. Hindle had pointed out, were isolated in the interior of their hosts and needed to be introduced in some way if the race was to survive. In the case of fungal parasites, however, the wind-borne spore constituted an easy means of infection and the need for heteroecism was much more difficult to comprehend.

PROCEEDINGS OF THE GENERAL MEETING ON 24 November 1949

Professor F. E. FRITSCH, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 27 October 1949, having been circulated, were taken as read and confirmed.

The President read for the third time the following alteration in the Bye-Laws, Chap, 1, Sect. 1, which was balloted for and adopted :—

That Bye-Laws, Chap. 1, Sect. 1, shall read :

> ' Sect. 1. The number of Fellows shall be limited to one thousand, exclusive of Honorary Members, Foreign Members and Associates. The method of election shall be by Ballot '.

The following were thanked for gifts made to the Library since the last Meeting :—Mr. Robert A. Bruce, Professor H. G. Champion, Mr. A. E. Gunther, Mr. R. E. Holttum, Dr. F. R. Irvine, Dr. A. J. T. Janse, H.M. The Emperor of Japan, Mr. Peter Scott, Capt. F. Kingdon Ward, and Professor F. E. Weiss, F.R.S.

The following Fellows signed the Obligation in the Roll and Charter Book, and were admitted Fellows :—Dr. Frederick James Fitzmaurice Barrington, Professor Arthur Roy Clapham, Mr. James Hartley Murgatroyd, Mrs. Mary Peach, B.Sc., Mr. William Victor David Pieris, M.A., B.Sc., Mr. Surendra Rohatgi, B.Sc., Mr. Leo Sachs, B.Sc., and Mr. Edmund A. C. L. E. Schelpe.

The President reported the following deaths :—Mr. Frederick William Mills and Mr. Stephen John Batchelder, Fellows of the Society.

A DISCUSSION ON MORPHOGENESIS was opened by Professors E. Ashby and C. W. Wardlaw, who read the following papers :—

Professor E. ASHBY and Miss E. WANGERMANN. Morphogenesis in *Lemna minor*.

Professor C. W. WARDLAW. Organogenesis in Ferns.

Professor G. R. DE BEER, F.R.S., made a contribution from the zoological standpoint.

(In the general discussion the following took part :—Professor A. R. Clapham ; Professor Wardlaw replied.)

The following papers were read in title :—

' A revision of the genus *Otiophora* Zucc. (Rubiaceae) '. By BERNARD VERDCOURT, A.L.S. [Printed in *Journal, Botany*, **53**.]

' Some Cornish *Rubi* '. By F. RILSTONE, A.L.S. [Printed in *Journal, Botany*, **53**.]

A DISCUSSION ON MORPHOGENESIS

MORPHOGENESIS IN LEMNA MINOR

By Elisabeth Wangermann and Eric Ashby
Department of Botany, The University, Manchester.

(With 2 figures in the text.)

The problems of ageing and rejuvenescence are of great interest in biology. They are difficult problems to study, largely because there are no simple and unambiguous ways to measure ageing. Physiological age certainly does not always correspond to time-age, and efforts to substitute other measures of physiological age have not met with wide success. The recent revival of interest in morphogenesis has focused attention on some very familiar features of plant growth which provide useful morphological symptoms of ageing. Juvenile leaves, for instance, whatever may cause them, are certainly symptoms of immaturity : they persist in conditions which delay sexual maturity and they are associated with phases of regeneration, as in cuttings. And, as we have recently shown, the consistent differences in shape between successive leaves on the stem of a herbaceous plant which accompany its development from a seedling to an adult, are certainly related to its physiological age and can in many instances be expressed quantitatively (Ashby, 1948 *a*, *b*). Changes in leaf shape are very sensitive to environmental factors which affect maturity, such as length of day (Ashby 1950) ; the normal sequence of shapes is entirely upset by conditions which bring on early flowering. Observations such as these suggest that an understanding of the causes of differences in shape between successive leaves might lead to an understanding of the causes of ageing.

The differences in shape of successive leaves might be due to causes other than ageing of the apical meristem : to differences in the external environment, for instance, or to the fact that upper leaves are further away from the root system than lower leaves (Ashby 1948 *b*). It has been necessary therefore for us to work with a plant where all such variables are eliminated except the ageing of the meristem.

Lemna minor is a suitable plant for this purpose. It can be grown under closely controlled conditions and successive fronds arise from the same location on the mother plant. For our purpose it is immaterial whether the fronds are morphologically leaves or phyllodes or cladodes.

The mode of growth of *Lemna* has been described by us in a recent paper (Ashby, Wangermann, and Winter 1949). The mother frond carries a double meristem with an expectation of life of about forty days. The number of daughter fronds produced by this double meristem depends partly on its genetical constitution, partly on the physiological age of the frond which produced it, and partly on the external environment.

For ' mother ' fronds we always use the third vegetative generation of first daughters, and we grow these under constant conditions in labelled compartments. The preliminary data on which our work is based are summarized in figure 1. The conclusions to which attention should be drawn are : (i) the limited expectation of life of a frond ; (ii) the approximately constant number of daughter fronds produced by a mother during this life ; (iii) the fact that each successive frond is smaller than the frond preceding it, even though they all come from the same meristem and have grown under the same conditions ; (iv) the fact that the expectation of life of successive daughters diminishes concurrently with their size.

We have here a clear case of a consistent change in size of successive daughter fronds accompanying the ageing of the mother frond. But in spite of this the average size of fronds in a colony does not progressively diminish, it remains about constant. This is due to the remarkable fact that the abnormally small daughter fronds, which appear late in the life of a mother frond, themselves have daughter fronds not smaller, but much larger than themselves. For instance a single fourth frond, only 1/5 the size of its mother, has a first daughter twice the size of itself. This is a clear case of rejuvenation, and it occurs in a constant environment (Ashby and Wangermann 1949). The differences in size are due to the number of cells, not to their size.

These are the basic facts which we have to interpret, and the experiments we have done since are attempts to analyse these basic facts.

We assumed that there might be as many as four different explanations of the gradient of diminishing size in successive fronds. These assumptions are :—(i) Late-formed fronds might be small because they arise from smaller initials than early formed fronds, and this might be due simply to the very restricted space available on a *Lemna* meristem. To examine this we cut sections through the meristems of mother fronds at different ages. We found evidence that a fourth frond initial is indeed smaller than a third frond initial ; but there is no reason to believe that a fourth frond initial is small because there is no room on the meristem for it to be any bigger. No conclusions can be drawn about the sizes of initials of first and second fronds because the fronds develop exponentially from the meristem with no resting period at all. (ii) Late-formed fronds might be small because their size depends on a supply of some growth promoting substance from the mother frond which diminishes as the mother frond becomes older, or alternatively : (iii) Late-formed fronds might be small because their growth is suppressed by some inhibitor from the mother frond which increases with age.

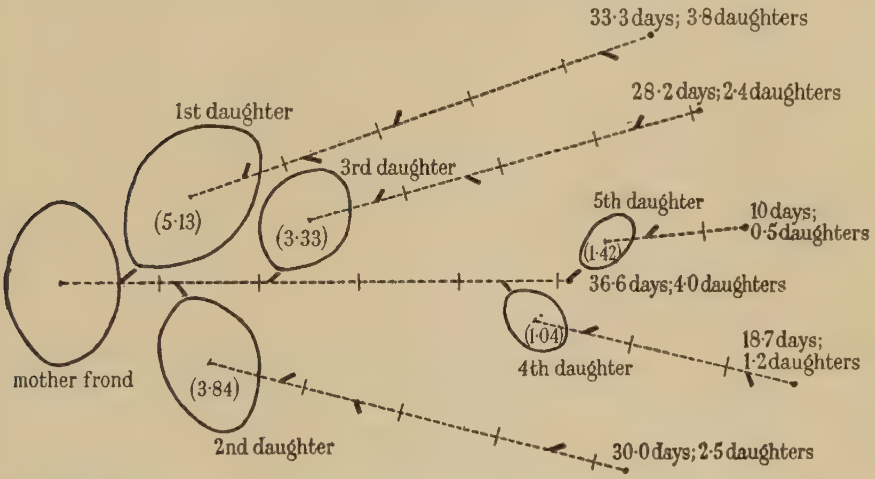

FIG. 1. Diagram to show areas (outlines with figures in brackets) and expectation of life (broken lines marked off in weeks, with figures at end) of successive daughters from one mother frond. All figures are means of 10 except those for fifth daughter, which are the means of two.

In order to distinguish between these alternatives—of growth promotion and growth inhibition—we dissected out daughter fronds at various stages of their growth, in order to determine what area they reached when detached from their mothers. The fronds dissected out, though small, were always green and even contained stored starch. They were not likely to be dependent upon the mother fronds for photosynthate or for mineral nutrients. We argued that on the one hand if it is a growth promoting substance which comes from the mother frond, then an immature detached frond would not reach normal area; on the other hand, if it is a growth inhibiting substance, then an immature detached frond would reach normal, or even supernormal area. Our experiments gave unambiguous results. Fronds detached at all stages show some growth, but on no occasion do they reach the final area of fronds still joined to the mother frond; and the amount of growth shown by a detached frond is the same whether it is at a high light intensity or just above the compensation point. This we take to be evidence that the effect of the mother frond on its daughters is to promote growth, not to inhibit growth. (iv) If the mother frond provides the daughters with growth-promoting substances, then it is possible that late-formed fronds might be small because earlier-formed fronds have monopolized the growth promoting substance. Experiments we have done to test this possibility indicate that it is unlikely to be true, but since the removal of early-formed fronds disturbs the plastochron intervals between later fronds, we are not yet able to interpret the experiments completely.

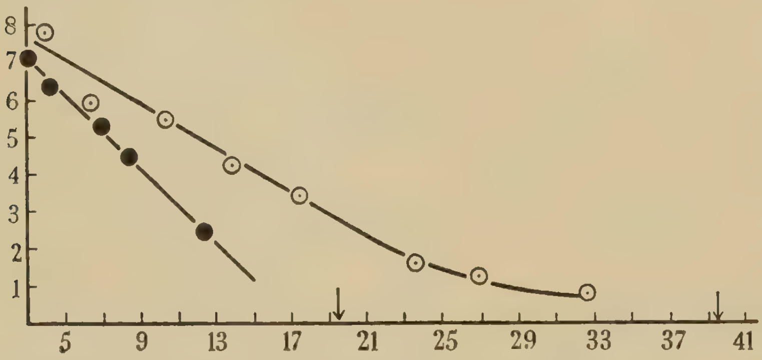

FIG. 2. Relation between frond area of daughter frond (ordinate), and age of mother frond at which daughter frond appeared (abscissa). ⊙———⊙ : fronds grown in normal culture medium; ●———● : fronds grown in culture medium with 2·5 mg./l of hetero-auxin added. Arrows show time of death of mother fronds.

We may summarize our interim conclusion about the cause of the diminishing size of successive fronds of *Lemna* by saying that it is not likely to be due to crowding of frond initials at the meristem, nor is it due to any inhibition from the mother frond as it becomes older. The results of our experiments are consistent with the view that the mother frond produces a substance which promotes the growth of daughter fronds, and which diminishes in quantity (or effectiveness) as the mother frond ages.

We next have to enquire how much of the mother frond is necessary to provide the growth promoting substance, and what the substance is. We have carried out two experiments which supply a little evidence on these questions. In the first of these experiments we studied the growth of first daughter fronds attached to parts of mother fronds. Our object was to determine how much of the mother frond is necessary to promote normal growth of the daughter. The results indicate clearly that the beneficial effect of the mother frond on a daughter frond remains even if some 80 per cent. of the mother frond is cut away. In the second experiment we grew normal mother fronds, and isolated young first daughter fronds, in culture solution containing 2·5 mg. per litre of hetero-auxin. Our main purpose was to discover whether an isolated frond would reach its full size in the presence of auxin. It does not do this; the final area of an isolated daughter frond was 4·13 mm² whereas daughter fronds attached to mother fronds reached an area of 7·83 mm². Of course one cannot conclude from an experiment at only one concentration of hetero-auxin that the growth promoting substance which the mother provides is *not* hetero-auxin or auxin, but it seems at any rate improbable. There was a second effect of hetero-auxin which is relevant to our discussion, namely that it *shortens* the expectation of life of a mother frond and accelerates the production of daughter fronds (fig. 2). This effect of hetero-auxin is very important for one of the main purposes of our study, for it enables us to test our hypothesis that the diminution in area from frond to frond is a measure of ageing. Hetero-auxin reduces the expectation of life from about forty days to about nineteen days: and it is evident from the graph that the rate of falling off of area is consistent with this. We present this as evidence that in *Lemna minor* the rate of diminution of area between successive daughter fronds is a measure of the rate of ageing of the mother frond. A full account of these experiments will be published in due course.

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ORGANOGENESIS IN FERNS: EVIDENCE RELATING TO GROWTH CENTRES AND PHYSIOLOGICAL FIELDS

By C. W. WARDLAW
Department of Cryptogamic Botany, University of Manchester.

(With 5 figures in the text.)

In the following notes experimental data which relate to the inception of leaf and bud primordia in ferns are considered.

The leaf primordia in leptosporangiate ferns such as *Dryopteris aristata* Druce are widely spaced round the base of the apical cone or growing point and constitute a regular phyllotactic sequence (fig. 1). Bud positions may be described as axillary or interfoliar. In studies of morphogenesis some explanation is required of the curious fact that whereas leaf primordia are formed, bud primordia are not, although the rudiments of both are histologically identical. By experimental methods, M. and R. Snow, following Van Iterson, have shown that the next leaf primordium to be formed at the shoot apex (I_1, in fig. 1.) arises in the 'next available space' on the meristem, i.e. in a position distant from the apical cell (or apical cell group) and in the widest gap above the top cycle of primordia. The writer's experiments with *Dryopteris* support this view. But in the ferns the new primordium occupies only a small part of the available space, i.e. in no sense can it be said that the primordia constitute a system of touching circles. Accordingly, it seemed necessary to account for the precise position between two primordia in which the new primordium is formed.

Certain experimental observations have led the writer to a reconsideration of views put forward by Schoute in 1913. With some modifications these afford a means of accounting for the positions in which new leaf primordia arise, for the inhibition of buds and for the regulated or harmonious development of the leafy shoot. Not least important, some of the relevant hypotheses can be tested by experimental means. Briefly, the hypotheses are these (fig. 1) : (1) the shoot-apex and the apex of each leaf primordium is a growth centre, round which a physiological field develops ; (2) a new growth centre cannot arise within an existing field, but can arise on the apical meristem outside it, i.e. the field has inhibitional properties. It is assumed that there is no fundamental metabolic difference between shoot and leaf apices. As the diagram (which is purely arbitrary in design) shows, the first area of the apical meristem which will become free from the inhibitive effects of existing fields lies between primordia 3 and 5, i.e. the I_1 position, in sequence with primordia 3, 2, 1 ; and the next will be the I_2 position, and so on. Bud sites or positions, situated between leaf primordia, will also be inhibited. According to this conception

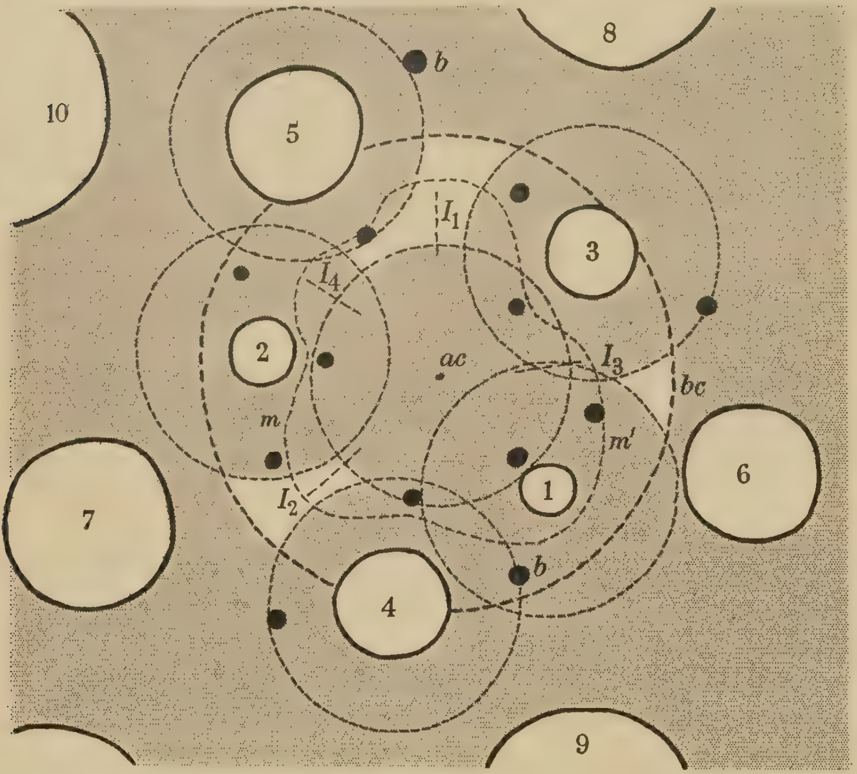

Fig. 1. Diagrammatic representation of a large apex of *Dryopteris aristata* as seen from above. The physiological fields of the top cycle of leaf primordia (*P*) (labelled 1–5 in order of increasing age) and of the apical cell group (*ac*) are indicated by circles. The next leaf primordium will be formed in the position marked I_1, the next again at I_2 ; positions I_3 and I_4 are also indicated. Bud positions (*b*) are indicated by black spots : m–m^1 indicates the lower limit of the apical meristem, which reaches a variable distance down the sides of the apical cone ; the approximate outline of the base of the latter, i.e. where it widens out into the broad sub-apical region is indicated by the broken circular line *bc*. (×30.)

older primordia will determine the positions of new ones and will exercise a controlling or regulative effect on them. If these ideas are valid, a leaf primordium, or a primordium site, which is isolated from the adjacent older primordia by vertical incisions (fig. 2), should show rapid relative growth and should become of abnormally large size. This prediction has been realized in many experiments.

A characteristic feature of the fern apex is that there is a development of leaf primordia whereas bud rudiments remain inhibited, i.e. in respect of organ formation. Experimental data contribute towards an understanding of this situation. It is being assumed that the meristematic cells in a leaf site or position lie outside the effective field of the apical cell group, i.e. they are sufficiently far away from the apical cell to grow out into a leaf primordium: but a comparable group of cells in a bud position, about the same level on the meristem, does not grow out to form a bud primordium. It appeared, therefore, that the inhibition of buds in these positions must be due to the adjacent leaf primordia and possibly also to those forming in the next cycle above. Experimental evidence was sought by observing the result when the top cycle of primordia (P_1–P_5) and the positions I_1–I_3 were punctured. New organs soon appeared in interfoliar positions in the cycle P_1–P_5 (fig. 3). These induced organs were leaves, *not* buds: they arose, like normal leaves, on the sides of the apical cone. In brief, by experimental means, it has been possible to make leaf primordia arise in what are normally bud positions.

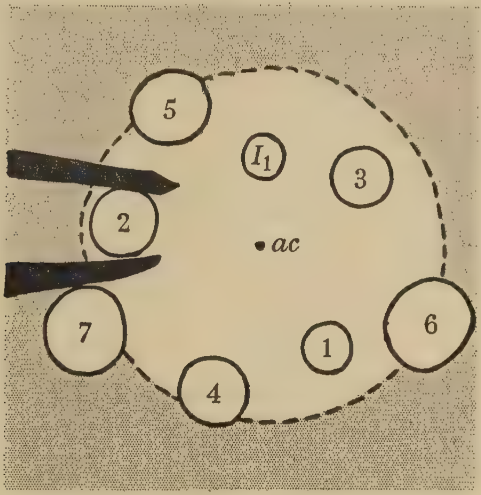

FIG. 2. Radial incisions (black) have been made on both sides of leaf primordium *2* thereby isolating it from the older primordia, P_5 and P_7: the isolated primordium soon becomes larger than older primordia. A new primordium has appeared at I_1. (×27.)

M. and R. Snow have stated that the space between existing primordia in which a new leaf primordium can arise must be of a certain minimal width. This view is compatible with the ideas and data now advanced, in that the space for the inception of a primordium must be sufficiently large so as not to be completely eclipsed by the inhibitive fields of the adjacent existing primordia. But the space needed for the actual site of the new primordium may be quite small. That this is so has been demonstrated by making parallel radial incisions close together on either side of the I_1, I_2 or I_3 positions.

Leaf primordia were formed in the narrow spaces between the incisions. These observations clarify certain aspects of the normal development that have long been obscure, at least to the writer, i.e. that the next primordium to be formed does, in fact, arise in the widest available space above the top cycle of primordia yet only occupies a small part of it.

Histologically, the rudiments of a very young leaf primordium and a very young bud primordium are identical. Leaf primordia are invariably formed on the sides of the apical cone, and are subject to the factors of growth at work there. Growth is considerably more rapid on the abaxial than the adaxial side and the latter may further be subject to inhibitive effects proceeding from the apical cell group. These factors may perhaps be held accountable for the characteristic dorsiventral symmetry of the leaf. But, in the normal development, buds are never formed on the apical cone: they always occur lower down on the maturing or mature shoot and their characteristic radial symmetry may tentatively be referred to the more symmetrical distribution of growth in the positions in which they arise. (No doubt this explanation is a considerable over-simplification of the differences between leaves and lateral shoots). In many experiments it has been observed that once a leaf primordium, with its characteristic two-sided apical cell, has been formed, it cannot be transformed into a shoot. By separating the I_1 position from the shoot apex by a tangential incision, however, a bud can be induced to develop there (fig. 4). *Thus, in ferns,*

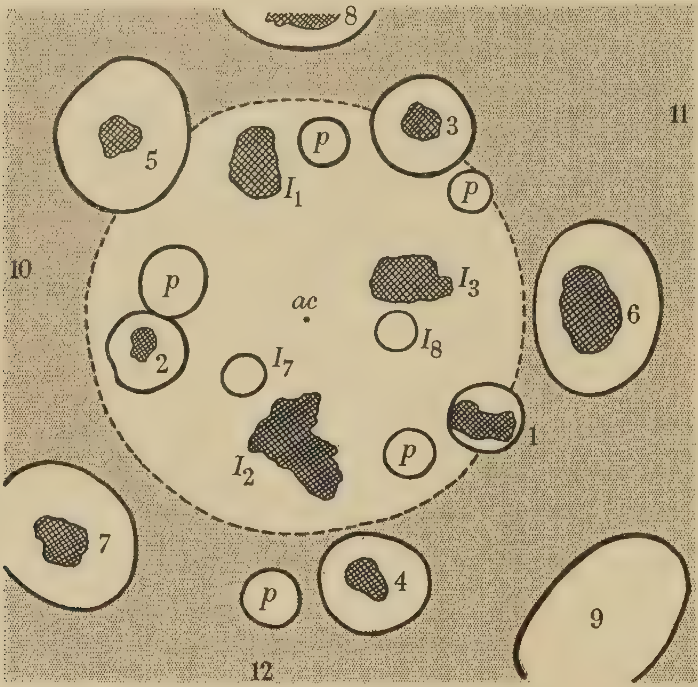

Fig. 3. The apices of P_1–P_5 and positions I_1–I_3 have been punctured (cross-hatched). Interfoliar leaf primordia (*p*) (and axillary to the older primordia P_8–P_{12}) have been formed in what are normally bud positions. No new primordia have arisen in the I_4, I_5 or I_6 positions, but two new primordia, above the cycle P_1–P_5 and labelled I_7 and I_8, are in approximately normal positions for these primordia. *ac*, apical cell. (×27.)

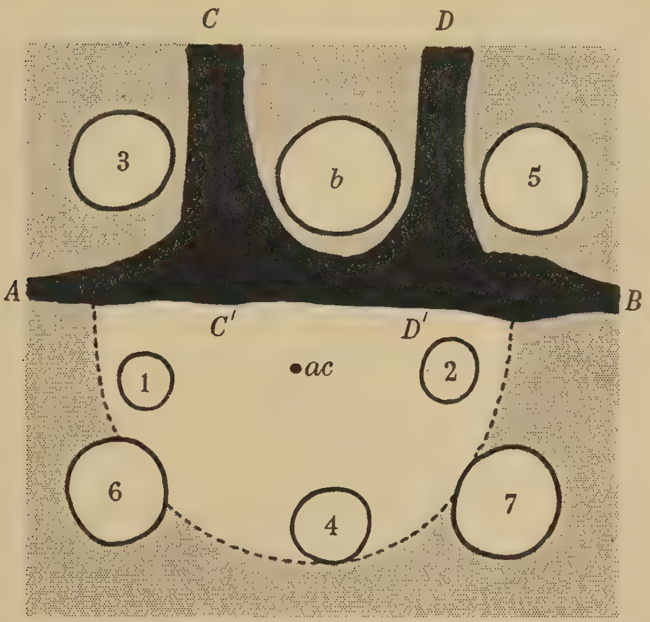

FIG. 4. The position I_1 has been isolated from the apical cell group by the tangential cut AB, and from the adjacent primordia P_3 and P_5 by the radial incisions CC^1 and DD^1. A bud (b) has been formed in the I_1 position, i.e. in what is normally a leaf position. Only the tangential incision is needed to produce this effect. ($\times 27$).

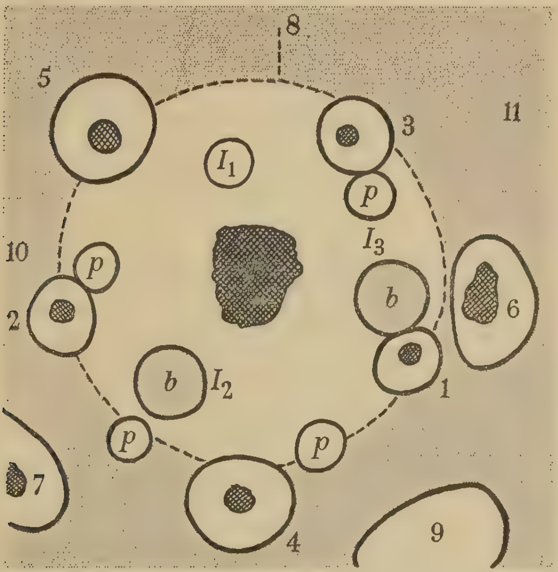

FIG. 5. The shoot apex and primordia P_1–P_7 have been punctured (cross-hatched). Various interfoliar leaf primordia (p) have been induced. But whereas a leaf primordium has been formed in the I_1 position, a bud (b) has been formed at I_2; a bud has also arisen above the axil of P_6 and there is no primordium at I_3. ($\times 27$.)

it has thus been possible to induce leaf formation in bud positions and bud formation in leaf positions, i.e. the whole of the apical meristem is totipotent in respect of the formation of its lateral members and the characteristic symmetry and structure of leaves and buds are due to the positions in which they are formed and to the factors of growth and related factors which are incident in these positions. Lastly, when the top cycle of leaf primordia and the shoot apex are punctured, either leaves or buds, in different instances, have been observed to arise in the I_1, I_2 and I_3 positions (fig. 5). From the records which have been obtained it is evident that very little is needed to tip the balance between leaf formation and bud formation at the fern apex.

References.

A full account of the work summarized above is available in *Growth* (Supplement) for 1949, and in the *Annals of Botany* for 1950. A summary account has appeared in *Nature.*

DISCUSSION BY PROFESSOR G. R. de BEER

Professor de Beer began by stating that ever since he had had the pleasure and privilege of being acquainted with the remarkable work of Mr. and Mrs. R. Snow on correlation and phyllotaxis, he had been impressed with the parallelism between the problems presented by these studies and those which were engaging the attention of students of experimental embryology.

In the short time at his disposal, he proposed to refer solely to the aspects which he had mentioned, namely, correlation and phyllotaxis. Mr. and Mrs. Snow and Professor Wardlaw had provided particular evidence of the power possessed by certain regions in the body of the plant organism to control or suppress the appearance of other structures within a certain distance. Among animals, this phenomenon is well known, largely thanks to the work of Professor C. M. Child, F.M.L.S. For instance, in planarians he has shown that the distance behind the head at which a pharynx develops is a function of the degree of development of the head itself. A well-developed head will not , as it were, tolerate the existence of the pharynx nearer to it than a certain distance ; but a poorly developed head may have a pharynx formed quite close to it. That this is an effect exerted by the head has been shown incontrovertibly by the experiments of Santos, who grafted heads of planarians into the sides of the body of other individuals and obtained the formation of a pharynx (or even sometimes two pharynxes) ; one above and one beneath the graft at certain distances from the graft.

A further example of the power of inhibition at a distance is proved by the work on the coelenterate *Cordylophora*, begun by Beadle and Booth and now confirmed and extended by Miss J. Singer in his Department. When fragments of *Cordylophora* are allowed to aggregate, the aggregated mass normally gives off a number of outgrowths, each of which regenerates into a polyp. But if to the aggregated mass there is added the oral cone of another individual, not only does the oral cone induce the formation of a polyp immediately beneath itself, but it inhibits the formation of other outgrowths and polyps. The parallelism here between the phenomena observed on botanical and zoological material is close and should well repay further attention.

In the striking work on the localization and formation of leaf-rudiments and buds, in flowering plants and in ferns, Mr. and Mrs. Snow and Professor Wardlaw have established the existence of a state of affairs usually described by the term ‘ morphogenetic field ’, the parallels of which are numerous in animal material. It has been shown that while the region surrounding the apex possesses a determination to form leaf-rudiments, the actual location of a leaf-rudiment is susceptible of modification and control by experimental methods. The same phenomenon is presented in animals by a large number of structures, of which the vertebrate limb is perhaps the best example.

It has been shown in amphibia that a region occupying a disc-like shape in the body wall of the flank at the level of the 3rd, 4th and 5th segments of the trunk, possesses a general determination to undergo development into an arm. There is however, at the early stages, no precise local determination of which cells will contribute which part of the arm. Indeed, from one arm-disc there may be formed two arms, and conversely, two arm-discs (provided that their orientations are consonant) can give rise to one arm. Further, if the arm-disc is removed altogether the resulting embryo is permanently armless. This means that more cells have the quality of being able to develop into an arm than do in fact produce an arm in normal development. Within the limb-disc there is still an indeterminacy as regards precise location of the future arm or arms ; the only thing that is determined is that if anything is developed at all, it will have the quality of an arm. This state of indeterminacy within an area which already possesses a general determination as regards its fate is usually described by saying that the rudiment represents a morphogenetic field. Within that field, the power of regulation is still present.

A further analysis of the properties of morphogenetic fields may be followed in the limb-bud of the chick. As Professor P. D. F. Murray has shown in a beautiful series of experiments, when the limb-disc has grown out into a conical bud, a regional determination into sub-fields has taken place. The proximal half of such a limb-bud when isolated, will, in the case of a leg, develop into a complete and nearly perfect thigh, without any shank. The distal half of the same bud can give rise to a perfect foot and shank. It is impossible to imagine that the cut of the scalpel separated precisely those cells which were determined to give rise respectively to thigh and shank, and it must be concluded that the limb-field has become sub-divided into morphogenetic sub-fields for the various segments of the limb, and that within these sub-fields, regulation takes place by means of the formation of the structure characteristic of that sub-field and the suppression of others.

In other experiments Professor Murray has been able to show that at a later stage, the proximal quarter of a limb-bud would give a perfect thigh, the next quarter would give a shank, and the distal quarter a foot.

The general principles which have been established for the limb-field have been found to apply to a large number of other morphogenetic fields in the vertebrate body, such as the neural tube, eye, lens, ear, hypophysis, nose, balancer, heart, gills and tail. The existence of such a diversity has made possible interesting experiments designed to investigate whether the cells of any given field can be made to differentiate into structures characteristic of other fields. In amphibia, the hand and the foot may easily be recognized by the number of digits, namely, four and five respectively. It was found by Milojevic that the regeneration-bud of an amputated arm when grafted on to the stump of an amputated leg will develop into a foot, provided that the regeneration-bud is not older than a certain critical age. If older than that age, it will develop in accordance with its original position, into a hand. This means that the quality which is impressed upon differentiating tissue is that of the field in which it is situated, and that after a certain time it becomes fixed in this determination.

Even more striking are the experiments of Guyenot in which a limb regeneration-bud grafted into the neighbourhood of the tail in a newt develops into a tail ; and conversely, as Weiss has shown, a tail regeneration-bud grafted on to the stump of a limb will develop into a limb.

The examples just given may throw some light on the problems raised by

Mr. and Mrs. Snow and Professor Wardlaw, particularly in regard to the possibility of inducing tissue in a morphogenetic field of one kind to undergo development into a structure characteristic of another. A further parallel to the induction of buds in leaf positions and leaves in bud positions is provided by the phenomenon known in the regeneration of animals as heteromorphosis. It is exemplified in the rock lobster which, after amputation of a stalked eye will only regenerate an eye if the optic ganglion is present in the stump: if it is absent, the structure regenerated on the stump is not an eye but an antenna. Another example is provided by the stick insect which after amputation of an antenna may regenerate a limb. More generally, those cases in which a hind end is regenerated instead of a head in worms, are further instances of induction of abnormal structures in place of normal ones.

REFERENCES.

References to the above-described experiments will be found in *The Elements of Experimental Embryology*, by J. S. Huxley and G. R. de Beer, Cambridge University Press, 1934.

PROCEEDINGS OF THE GENERAL MEETING ON 5 January 1950

Professor F. E. FRITSCH, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 24 November 1949, having been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last Meeting:—Rear-Admiral Tufton Beamish, C.B., Miss Helen T. Dymes, Mr. R. Morse, Mr. A. A. Prestwich, Mr. Christopher Sandeman, Dr. Eduard Thommen, Dr. C. Wesenberg-Lund, F.M.L.S., and the Royal College of Surgeons of England.

The following Fellows signed the Obligation in the Roll and Charter Book, and were admitted Fellows:—Dr. Lionel Percy Clarke, Mr. Peter Hadland Davis, Prof. Peter Brian Medawar, F.R.S., and Mr. Harry Stansfield.

The President reported the following deaths:—Mr. Robert Wilfred Inder and Mr. Edmund Gilbert Baker, Fellows; and Prof. Richard Woltereck, Foreign Member.

The following communications were read and discussed:—

Professor J. MCLEAN THOMPSON. A contribution to our knowledge of the Swartzieae; with special reference to *Swartzia pinnata* Willd. (Discussed by Prof. F. E. Weiss, F.R.S., Dr. E. M. Delf, Prof. R. E. Holttum, Mr. E. J. H. Corner, Mr. I. H. Burkill, and the President; Prof. McLean Thompson replied.) [To be printed in full in Part 2.]

Mr. B. D. WRAGGE MORLEY. Neurotic behaviour in ants. (Discussed by Mr. H. St. J. K. Donisthorpe, Dr. E. M. Delf, Prof. G. D. Hale Carpenter, M.B.E., and the President; Mr. Wragge Morley replied.)

Abstract,—

Neurotic behaviour in one of a colony of large Black Ants (*Formica fusca*) was observed whilst demonstrating to a friend how an ant runs through an experimental maze. This ant had just completed an experimental run in the same maze and had only been back again with its comrades in the observation nest for a few minutes. When it was put into the maze for the second time it started to show twitching movements of its feelers and legs. It soon started off to run through the maze, which it normally did in about forty to fifty seconds without making a single mistake. Unfortunately on this occasion, when it got halfway through, it hesitated and made a mistake. Its limbs and feelers twitched spasmodically while it kept on trying to get through the wall of the cul-de-sac. These spasmodic jerkings got worse as the ant became more excited, and it soon started to circle backwards while still showing bad twitching movements, and eventually collapsed and became unconscious. This ant recovered when placed under a cold-water tap for a few seconds.

Since then I have observed several cases of comparable breakdown in ants and I have found a variety of ways of producing this sort of nervous breakdown in these insects.

This paper describes these experiments and how they were linked with comparable experiments on some vertebrate animals.

PROCEEDINGS OF THE GENERAL MEETING ON 19 January 1950

Professor F. E. Fritsch, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 5 January 1950, having been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Professor Dr. Alfred Ernst, F.M.L.S., Professor Lily Newton, Mr. Christopher Sandeman, Mr. W. T. Stearn, Dr. J. C. Willis, F.R.S., and the Lund Botanical Exchange Club, Lund.

The President announced that the Fellows of the Society were invited to send in nominations for the Officers, the Linnean Medallist (Botanist), Foreign Members and Associates *honoris causa*. Such nominations should be sent to the Assistant Secretary before 17 February 1950.

A Discussion on the Evolution of Locomotory Mechanisms in Arthropods and Worms, was opened by Dr. S. M. Manton, F.R.S., and Dr. C. F. A. Pantin, F.R.S.

In the general discussion the following took part :—Prof. G. D. Hale Carpenter, M.B.E., Mr. I. H. Burkill, Dr. J. P. Harding, Prof. A. J. E. Cave, Prof. Doris L. Mackinnon, Mr. G. E. H. Foxon ; Dr. Manton and Dr. Pantin replied.

DISCUSSION ON THE EVOLUTION OF LOCOMOTORY MECHANISMS IN ARTHROPODS AND WORMS

THE EVOLUTION OF THE LOCOMOTORY MECHANISMS OF THE ARTHROPODA*

By S. M. Manton.

The locomotory movements of many Arthropoda are closely associated with their body form, and animals of similar structure generally perform gaits of the same type. It is probable that structural features concerning the shape of a segment, the number of segments in the body, the length of a leg relative both to the dimensions of the segment and to the lengths of the other legs, the equal or alternating size of tergites or their fusion together, and the types of muscular, respiratory, vascular and nervous systems, have all evolved simultaneously with the evolution of locomotory movements. A study of locomotory movements may provide in some measure a functional explanation for the evolution of body form within the various groups of arthropods, and also an indication of some functional aspects concerning the origin of the Arthropoda from the Annelida.

The soft bodied Onychophora today lack striated muscle and a rigid integument, and in many ways represent a stage through which the hard bodied Arthropoda must have passed. In contrast to the Annelida, the propulsive force in Peripatus is provided by the extrinsic limb muscles, and not by the body musculature, which in Peripatus supplies a fairly firm attachment for the limb muscles. The body does not undulate. Three gaits are predominantly used for progression at different speeds, and their employment is accompanied by changes in body length as the gait and speed is altered. Such a mechanism was probably evolved in a marine environment. It represents a functional advance on the annelidan methods of locomotion, where increase in the speed of crawling is associated, in polychaetes possessing well developed parapodia, with an increase in lateral undulations of the body, a method involving a waste of locomotory force in side to side movements. Some polychaetes raise their bodies as far from the ground in walking as do many arthropods, and the evolution of the Onychophoran locomotory mechanism by such an annelid would eliminate the waste of effort created by side to side movements, and would probably be accompanied by a ready alteration in body extension. The latter may have been correlated with the simultaneous elaboration of the haemocoel. A soft bodied Arthropod might thus be evolved with a faster gait than its annelidan ancestor.

The Onychophoran locomotory mechanism has the potentialities of further elaboration into the more specialized but less flexible gaits of the stiff bodied Arthropoda, none of which can execute the wide range of gaits performed by Peripatus. The morphological alterations which have been made by the several groups of stiff bodied Arthropoda in association with the type of gait which each employs are such that a gait once adopted, cannot readily be altered, except within narrow limits, so that the various methods of running become mutually exclusive. The evolution of striated muscle leads to an increase in the speed, but the presence of a rigid integument, necessitated by a quick moving arthropodan muscle, makes alterations in the extension of the body impossible, and the speed changing mechanism by alteration of the gait becomes less extensively used. Alterations in the duration of the pace, which remains almost constant in Peripatus, become the major method of varying the speed, and the gait within some groups changes but little.

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* A full account of this work is in course of preparation. Part I, The Locomotion of Peripatus. *Journ. Linn. Soc. London*, Zool. 1950, *41*, 529–570, 2 pls., 9 text-figs.

The Diplopoda have exploited the ‘ bottom gear ’ type of Onychophoran gait, the emphasis being on a powerful rather than a speedy gait. With the long backstroke is associated a short segment, and a frequent development of a large number of body segments. The formation of diplosegments by fusion provides a mechanism counteracting waste of effort by dorso-ventral undulations at the higher speeds. The Symphyla resemble the Diplopoda in many respects, but differ from them in others. The Geophilomorph and Scolopendromorph Chilopoda have elaborated the ‘ middle gear ’ gait of Peripatus, ultimately gaining considerable speed by a quickening of the backstroke. This gait is associated with a more elongated segment, and where the legs are fairly long and the backstroke very short, an alternation in the size of the tergites reduces the tendency towards lateral undulations which are wasteful of effort. Some Diplopoda have secondarily increased their speeds and developed a facies approaching that of the Chilopoda in some respects, while a few Chilopoda appear to have become content with slow locomotion and have correspondingly assumed some Diplopod-like features in association with their gait. The Lithobiomorph and Scutigeromorph Chilopoda have progressed further than the Scolopendromorpha in the evolution of speed, but in an entirely different manner, combining the ‘ top gear ’ gait of Peripatus with much longer legs. The longer legs introduce many problems which are met by a shortening of the segment and a reduction in the number of segments ; and an increased tendency towards lateral undulations is countered by an increase in the difference between the lengths of the tergites and by their fusion together as an *Scutigera*. The Pauropoda show much in common with the Scolopendromorpha and Insecta, and like them must have originally adopted a gait resembling the ‘ middle gear ’ of Peripatus. Time did not permit of a further consideration of other groups of Arthropoda, but it may be said that the Arachnida, Insecta, and many higher Crustacea gain speed mainly by an increase in the length of the leg, as in the Lithobiomorpha and Scutigeromorpha, but they have gone further than these chilopods in solving the common problems resulting from longer legs. Some of the difficulties dependent upon the possession of many long legs can only be eliminated if a smaller number of long legs are situated anteriorly on consecutive segments which are either fused together or lack mobility in certain planes. These features, together with the tendency to reduce or eliminate the segments at the posterior end of the body, are common to the Arachnida, Insecta, and Malacostraca. With a reduction in the number of walking legs, certain changes in the gaits become inevitable, and some gaits appear which are not performed by any of the many-legged arthropods. The correlation between the morphology and the gaits employed by the various groups of Arthropoda indicates that these animals must have evolved independently for a very long period of time, perhaps since a soft bodied stage.

LOCOMOTION IN BRITISH TERRESTRIAL NEMERTINES AND PLANARIANS: WITH A DISCUSSION ON THE IDENTITY OF RHYNCHODEMUS BILINEATUS (Mecznikow) IN BRITAIN, AND ON THE NAME FASCIOLA TERRESTRIS O. F. Müller

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(Plates **1** & **2** and 4 text-figures.)

Part I. Locomotion.

The worms we shall consider are the terrestrial nemertine *Geonemertes dendyi* Dakin (Pl. **1**), an immigrant to Britain from Western Australia (Pantin, 1944), the common British land planarian *Rhynchodemus terrestris* (O. F. Müller),

(=*Fasciola terrestris* O. F. Müller), (Pl. **2**, figs. 1–4), and a land planarian new to Britain identified as *Rhynchodemus bilineatus* (Mecznikow). A discussion of the identity of this last interesting animal and the necessity of giving O. F. Müller's *Fasciola terrestris* a new generic name is given in Part II of this paper. Specimens of all the worms were obtained from woods near Plymouth, and of the *Rhynchodemus* species from a wood near Cambridge also. It will be convenient first to describe the different methods of locomotion in these animals and then to draw some general conclusions.

Gliding in Geonemertes dendyi.

If this worm is placed on a glass plate it starts to glide along at a steady pace of about 7 to 10 mm. per minute. Careful observation of its ventral surface through an inverted plate makes clear that gliding is not due to small muscular waves such as Wilhelmi (1909) has described in aquatic planarians. On the other hand, the whole body is covered with cilia beating from head to tail. When the animal is immersed in water it is easy to see that these cilia drive the animal along. On land, locomotion remains 'aquatic'. Mucus is abundantly secreted; particularly over the whole of the head region. This is carried back by the cilia and the animal thus swims forwards in a tube of its own mucus. Such a tube is left as a trail behind the animal. On a clean glass plate its presence is readily made visible by rocking gently in a fine suspension of charcoal. The commercial product 'Charkaolin' is excellent for this purpose. Pl. **1**, fig. 1, shows such a track.

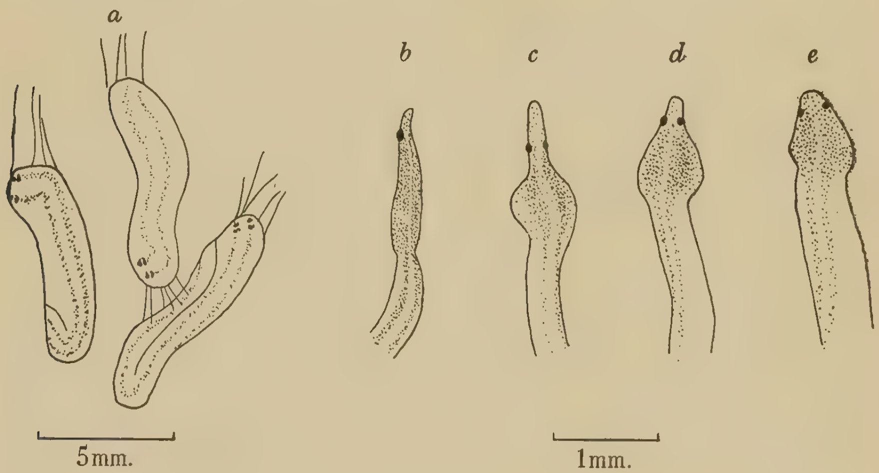

FIG. 1.

a, Geonemertes dendyi turning within slime cocoons.
b–e, Rhynchodemus bilineatus, successive figures from photographs during antiperistaltic contractions of cephalic hood during its adhesion to the substratum.

This method of progression makes great demands upon the water reserves of the animal unless it is in its own natural very humid habitat. In the dry air of a laboratory the worm steadily loses volume and soon ceases to move. Examination of it in this state shows that it has the power of toughening the layer of mucus which surrounds it into a 'slime cocoon'. This is transparent, and only the inactivity of the animal may betray its presence. It is however very sticky, and may well allow transport of the animal by foraging birds, to which it could adhere as easily as it does to a collector's fingers. The cocoon is rendered visible by a charcoal suspension (Pl. **1**, fig. 4).

When in the cocoon, the animal may become active and it can be seen to turn round within its enclosing membrane (text-fig. 1*a*). Stimulation leads to escape, apparently by local solution or digestion of the cocoon at the point where the head of the animal happens to be. Pl. **1**, fig. 3, shows a specimen escaping from its cocoon.

Whereas cilia provide the motive power, the direction of locomotion is governed by muscular action. The worm continually moves its head slightly from side to side as it glides along. Pl. **1**, fig. 2, shows small alternate waves of mucus left on each side of the trail as the animal glides along. Stimulation greatly increases these lateral movements and the most effective stimulus is light. Like the larva of *Calliphora* these animals are negatively photoklinotactic (Fraenkel and Gunn, 1940). By varied angular swinging of the head they come to turn directly away from a source of light. In Pl. **1**, fig. 1, the animal was placed in a plate in front of a lighted window. It emerged from its slime cocoon and glided away from the light. When nearing the end of the plate this was reversed. The oscillations of its head increased and quickly its path swung round until again it travelled away from the light.

The escape reaction of G. dendyi.

It is remarkable that a terrestrial organism should retain a ciliary locomotor mechanism, not only because of the difference of the medium but also because as a means of progression it is extremely slow in a world of very active predators, The animal however possesses a very effective escape reaction ; by means of the proboscis.

The nemertine proboscis is a very useful organ of varied function in different species. In the predatory *Cerebratulus lacteus* Wilson (1900) has shown that it is used as an exploratory tactile organ and also as a prehensile organ in feeding. The very much smaller *G. dendyi* possesses a relatively very much larger proboscis. The proboscis is used for escape as is also the case in *G. hillii* (Hett, 1924). It is not used in normal locomotion as Willemoes-Suhm (1874) states it to be in *G. agricola*.

As in many worm-like animals, very slight tactile stimulation of *G. dendyi* causes slight longitudinal withdrawal of head or tail. But stronger handling causes a sudden eversion of the proboscis. In fresh specimens this is shot out to twice or three times the length of the worm, and my observations suggest that the animal sometimes directs the proboscis towards dark objects near at hand.

Extrusion of the proboscis is shown in Pl. **1**, figs. 6 to 12. It is difficult to get the reaction more than once or twice in animals handled in the laboratory. Accordingly, flash-light photos were taken of numerous worms when they first showed the reaction and the figures in the plate represent different worms in which the exposure has caught different phases of the response. The photos were taken in a dimly lighted room. The release for the ‘ Bulb ’ exposure was connected by a mechanical device which fired a ‘ sashalite ’ bulb soon after the shutter opened.

Pl. **1**, fig. 6, shows an unstimulated worm. When the animal is stimulated to extrude the proboscis, there is a sudden simultaneous contraction of the whole of the circular muscle of the body. This results in an abrupt elongation of the worm to nearly twice its original length. The sudden elongation often throws the worm into curves at the hind end (Pl. **1**, figs. 7 and 8). In exhausted worms this may be all that occurs, but in normal worms, the elongation is accompanied by violent extrusion of the proboscis as in the Plate. Eversion takes about ¼ to ½ a second.

The proboscis now adheres to the substratum by its distal end, and a wave of longitudinal contraction and circular relaxation runs forward over the animal and its proboscis so that the animal flies forwards as in figs. 9 and 10. In these two figures the end of the proboscis fell just outside the plate of the camera. The flight forward takes from $\frac{1}{4}$ to 1 second. It slows up rapidly as the animal flies forwards.

The end of this stage is seen in Pl. **1**, fig. 11. The rhynchostome is now widely opened and the proboscis stowed back in the rhynchocoel. The proboscis is withdrawn from its distal end. The final stage in which the worm is extremely short and wide, the rhynchostome has been opened and the proboscis almost completely stowed away, is seen in Pl. **1**, fig. 12. This stage is slow and takes 2 to 5 seconds.

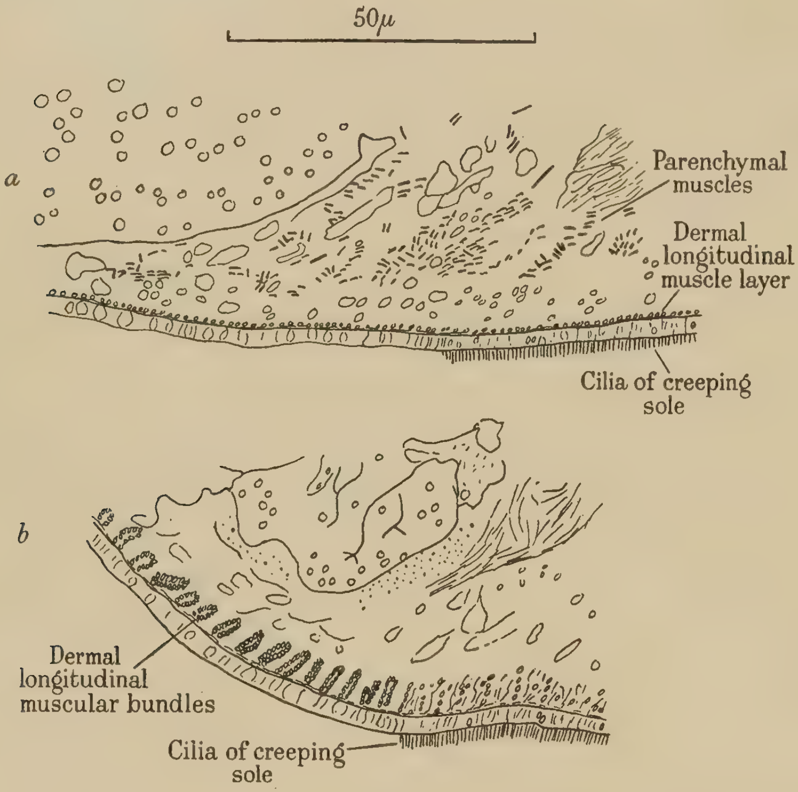
50μ
a
Parenchymal muscles
Dermal longitudinal muscle layer
Cilia of creeping sole
b
Dermal longitudinal muscular bundles
Cilia of creeping sole

FIG. 2.

a, R. terrestris. *b, R. bilineatus.*

Left-hand edge of ventral creeping sole, to show absence and presence of longitudinal muscular bundles. Camera lucida.

Normal locomotion in Rhynchodemidae.

Wilhelmi (1909) noted that in the large aquatic planarians, locomotion takes place through numerous fine muscular waves passing from head to tail along the ventral surface. The surface is ciliated and mucus is conveyed along it. Stringer (1917) showed that it was the muscular waves, and not the cilia which supplied the prime mechanical locomotor force.

Bresslau (1928) found that on a damp substratum the land planarian *Geoplana notocelis* moved by means of numerous small muscular waves running back along the ventral surface as in fresh water species. Under dry conditions the waves became slower and larger till it progressed by a succession of large muscular swellings, which passing back along the body made isolated points of contact with the substratum.

In *R. terrestris* and *R. bilineatus* locomotion takes place on somewhat the same plan. It is effected through the agency of a specialized creeping ‘ sole ’ running along the ventral surface. Cilia are restricted to this ventral sole (text-fig. 2), in contrast with the general ciliation of *Geonemertes*. Much mucus is secreted into the sole and carried back along it by the cilia as the animal moves along. In *R. terrestris* secretion laden cells are to be found in the parenchyma and appear to pass their secretion to the surface particularly just behind the head (text-fig. 3*b*). The cells and their secretion stain strongly with aniline blue in Mallory’s triple stain, and with light green in Masson’s Ponceau Light Green method.

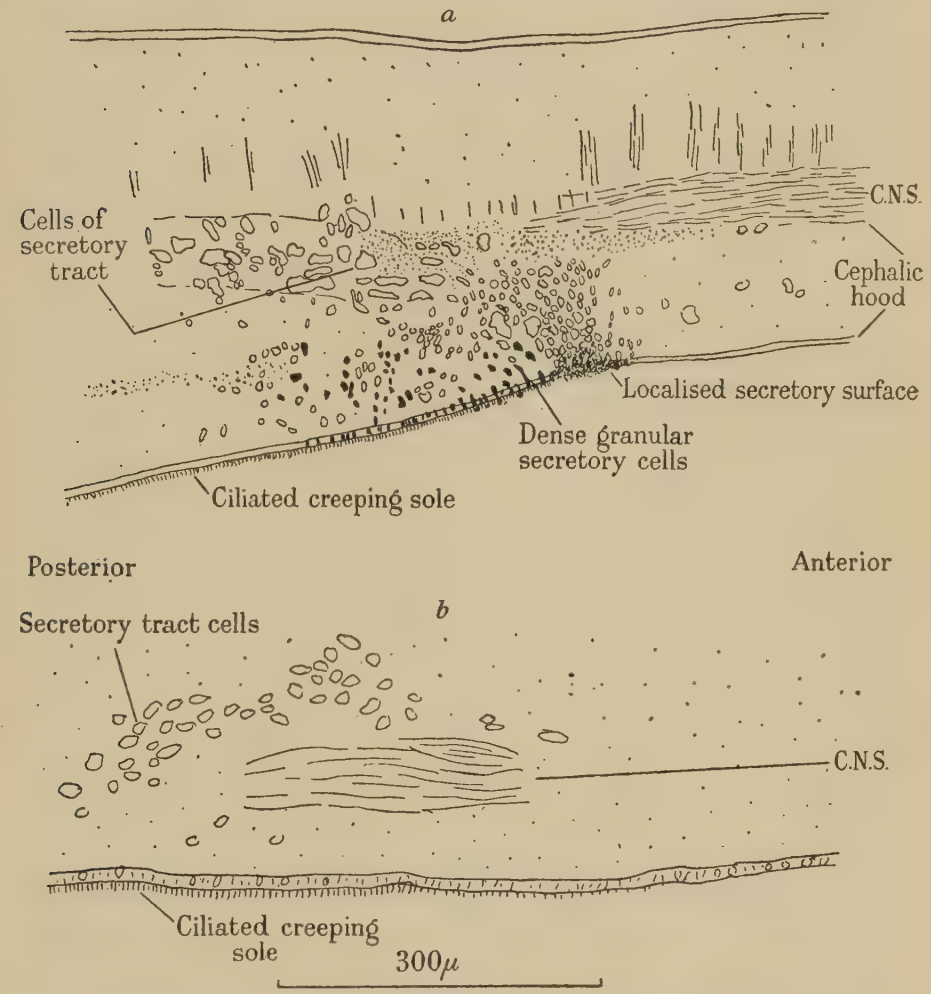

FIG. 3.

a. Sagittal section through neck region of *R. bilineatus* showing localized secretory surface at beginning of creeping sole, and two types of secretory cells : acidophil cells of the secretory path in the parenchyma, and densely granular cells just behind the secretory surface. Camera lucida.

b. Sagittal section of ventral surface of *R. terrestris* in corresponding region to *a*, showing absence of differentiated hood and of localized secretory surface. Camera lucida.

Pl. **2**, fig. 2, shows *R. terrestris* moving over a glass plate. A mucus trail can be seen behind. The normal speed is 2 to 3 cm. per minute. The head is slightly raised and moves from side to side, more evidently than in *G. dendyi*. As in the latter, the direction of locomotion is controlled through negative photoklinotaxis. Pl. **2**, fig. 3, shows the mucus trail of a specimen, rendered visible by finely divided carbon.

Though the direction of locomotion is controlled in the same way as in *G. dendyi*, the mechanism of locomotion is different. As in *Geoplana* and the freshwater Turbellaria waves of muscular contraction pass backward along the ventral surface. In *R. terrestris* they develop just behind the head and are confined to the creeping sole. The waves are however not very numerous, so that at any moment most of the sole is in contact with the substratum. As can be seen from the Plate, mucus is poured out from near the neck onto the creeping sole and the animal glides along leaving a slime trail. As the waves run back along the sole, the animal glides forward at about the same rate. Consequently at the front end of the animal the waves seem more or less stationary in relation to the substratum as the worm glides by. But the posterior part of the sole sweeps over the whole trail so that the mucus trail remaining after passage of the worm is continuous. On a dry substratum less mucus is secreted but the trail is still continuous (Pl. **2**, fig. 3). I have not seen *R. terrestris* progress by large isolated contraction waves only touching the substratum at isolated intervals as described by Bresslau (1928) in *Geoplana* : though one can imagine the development of these by great exaggeration of the waves and limitation of their point of contact with the substratum. This very kind of locomotion is in fact to be seen in a peculiar and highly developed condition in *R. bilineatus* (Pl. **2**, figs. 6 and 7).

In *R. bilineatus* locomotion is faster than in *G. dendyi* or *R. terrestris*. At 18° C. animals 12–13 mm. long travel some 5 cm. a minute. The body shows a regional specialization in relation to locomotor activity. The anterior quarter of the body is developed into a remarkable cephalic hood (Pl. **2**, figs. 5 to 14 and text-fig. 1, *b–e*). In locomotion this is held clear of the substratum, and as soon as locomotion begins, it starts to sway actively from side to side. Pl. **2**, fig. 12, shows a specimen beginning to walk from rest. The exposure was 1/25th of a second and the oscillation of the head has caused lateral blurring of its image.

Cells laden with secretion are numerous in the parenchyma of *R. bilineatus* and form a fairly well defined tract. In this species the secretory tract reaches the ventral surface just at the base of the neck and secretion pours out from a localized area almost as from the orifice of a gland (text-fig. 3). At this point, the ciliated epithelium of the sole, only weakly developed beneath the cephalic hood, suddenly becomes strongly developed as the creeping sole. The cells of the secretory path stain strongly with aniline blue in Azan and Mallory staining. In addition there are granular secretory cells of a different kind which add their secretion just behind the localized secretory surface. This specialized surface and marked local differentiation of gland cells is not evident in *R. terrestris*. Unlike *R. bilineatus*, sagittal sections of this animal show no abrupt transition as the sole passes from the belly to the cephalic hood (text-fig. 3 *b*).

During locomotion the creeping sole of *R. bilineatus* is thrown into a succession of large ventral protuberances which begin to develop just behind the neck, as seen in the lateral view, Pl. **2**, fig. 6. The moving worm is seen above its own reflection in the glass plate on which it walks. The protuberances pass backwards along the sole. Only their tips touch the substratum, so that the animal may almost be said to move by a succession of ‘ pseudopodia ’, or ‘ myopodia ’ developed at the neck and passing down the body. The commencing development of one of these myopodia can be seen in the Plate. As the worm glides forward the successive myopodia leave well-defined ‘ footmarks ’ (Pl. 2, figs. 6 and 7).

This method of locomotion is much more economical of mucus than that of *R. terrestris*. *R. bilineatus* is to be found in distinctly less damp situations than *R. terrestris*. It will be seen that the ‘ footmarks ’ tend to settle into an alternating right–left pattern (Pl. 2, fig. 6). This is because in undisturbed locomotion a new myopodium tends to coincide with each swing of the head region right and left. On damp substrata, the mucus ‘ footmarks ’ may be joined to a greater or lesser extent by a connecting thread of mucus. As the animal glides forward and the tail finally leaves the last footmark it may remain connected with it by the stream of mucus passed down the ciliated sole. Such a thread can be seen at the tail in Pl. 2, fig. 9. As Lehnert (1891) has pointed out, the continually produced mucus thread can be used by the animal to lower itself through the air from one object to another, after the manner of a spider.

The myopodia of *R. bilineatus* seem derivable from muscular waves such as occur in *R. terrestris* or indeed in the aquatic flatworms. But the mechanical system is highly specialized. Muscular waves running back along a ventral surface in contact with a continuous mucus trail on the substratum as in the aquatic planarians, seem to present mechanically a different system of locomotion from the isolated myopodial progression of *R. bilineatus*. Whereas in the former case it is perhaps easy to envisage a way in which the waves acting on the mucus trail might drive the animal forward, myopodial progression is obviously more complex.

In *R. bilineatus* the myopodial waves are not primarily waves of contraction, but waves of controlled local relaxation and lowering of tone permitting local extension of the creeping sole, presumably under the tonic pressure of the muscular body wall. If *R. bilineatus* is viewed by oblique light under a high power from beneath when walking over a glass plate, it is seen that as the animal goes by, the ciliary sole actively dives onto the substratum, passes along the mucus foot-mark and then leaves the substratum. The fact that the body surface in contact with the stationary foot-mark is moving forward over it is in striking contrast to the condition in some Gastropods, such as *Helix* sp. (Lissman, 1945), where the points of contact of the muscular waves with the substratum are stationary. We shall return to this point.

The force causing forward movement of the sole where this touches the foot-mark is due either to the muscular movement of the myopodia, or to ciliary activity or to the co-operation of both. It is not due to any still finer system of muscular waves running over the body surface. Like the rest of the body, the sole contains many small flecks of pigment, and when the animal is observed walking on an inverted glass plate, any relative movement of these flecks could at once be detected.

On the other hand such observation brings to light the fact that the cilia as well as the muscular waves play some part in the locomotor process. During normal locomotion metachronal ciliary waves can be seen passing along the sole from behind forwards at about 100μ per second. The distance between their crests is about 20μ and the frequency of the beat is near the flicker-rate. The direction of the ciliary beat is opposed to the metachronal wave and runs back along the creeping sole in the same direction as the myopodial waves.

If the animal stops moving, the ciliary waves are seen to flicker and cease. Resumption of locomotion is accompanied by restarting of the ciliary waves. The cilia are in fact under the control of the animal. The first sign of locomotion is an elongation of the body, followed by activity of the cilia and the muscular waves. Any contraction of the body in length whether the result of a stimulus or not appears to inhibit both cilia and muscle waves.

I have shown elsewhere (Pantin, 1947) that the cilia of the protonephridia of *Geonemertes* are under the control of the animal. Carter (1926) found that in gastropod veligers their intermittent ciliary activity became continuous under the action of drugs which prevented the periodic inhibitory action of the nervous system. If *R. bilineatus* is subjected to 5 to 10 per cent. ethyl alcohol, the muscular waves rapidly disappear and the whole muscular system becomes paralysed. The cilia of the sole however, now continue to beat rapidly and without inhibition. An animal in this state laid upon its sole on a glass plate creeps forward by ciliary action. But the movement is so slow that it is scarcely perceptible.

The cilia are of undoubted indirect importance for locomotion in carrying mucus back along the sole. How far they are of direct importance, by providing the actual locomotor force, is more difficult certainly to determine. Their very weak locomotive power when muscular action is paralysed by alcohol suggests that their contribution in normal locomotion is limited. On the other hand the passage of a myopodium, in contact with a mucus foot-mark, backwards along the body of the animal would undoubtedly generate some forward thrust. At the anterior edge of the foot-mark where the sole is continuously withdrawing from contact there will be a negative pressure pulling the surface of the myopodium forward whilst at the posterior surface of the foot-mark, where the sole is continuously thrusting into the foot-mark there will be a positive pressure pushing the surface of the myopodium forward. In such a system, the cilia might play a very important part, apart from any direct locomotor effect they may have. If there were no active cilia and movement took place solely through the action of the muscular waves, work would have to be done in sliding the sole forward against the viscous mucus of the foot-mark. But since in fact the cilia carry a sheet of mucus continuously backward along the sole the action of the cilia reduces the effective friction between the moving sole and the substratum towards zero, thereby increasing the efficiency of muscular action, perhaps greatly.

This co-operation between cilia and muscular action may account for one of the most striking differences between locomotion in planarians and locomotion in the foot of Gastropod molluscs such as *Helix* spp. The general resemblance of Turbellarian and Gastropod progression through the agency of muscular waves in a pedal muscular mat is well known. But, compared with *Helix*, the direction of the waves is reversed. In *Helix* and some other species the waves run forwards along the foot and the surface remains in fixed contact with the substratum except where the muscular wave pushes it forward (Lissman, 1945). In *R. bilineatus*, the waves run backwards and by the co-operation of muscular and ciliary action the animal continuously slides forward over each point of contact with the substratum. It would be interesting to compare this with such Gastropods as *Littorina littorea* in which the locomotor waves also are retrograde.

Other methods of progression in Rhynchodemidae.

On strong stimulation, many planarians exhibit a leech-like progression by alternate extension of the body followed by anterior adhesion, and then contraction of the body followed by posterior adhesion. Behaviour of this kind has occasionally been seen in *R. terrestris* though chiefly confined to the posterior part of the body. The contractions take the form of large antiperistaltic waves running from behind forwards. It is interesting to note that if such antiperistaltic waves became smaller and more numerous we should have in this animal a progression by muscular waves essentially resembling that of *Helix* spp. : the waves running forwards in the reverse direction from the myopodial waves of *R. bilineatus*.

In *R. bilineatus* the hood plays an important part in sudden and unusual movements. The hood is a highly organized structure. Normally it somewhat resembles the hood of cobra (Pl. **2**, fig. 5). It is leaf-like with the lateral edges turned a little down so that the under suface becomes a longitudinal groove (Pl. **2**, fig. 9). The whole structure is highly flexible. It can become long and thin (Pl. **2**, fig. 11), or may rapidly flatten out, as in Pl. **2**, fig. 10, where it is in contact with the substratum. It is used as a sucker for adhesion particularly when the animal is trying to make contact with the substratum under mechanically difficult conditions, as when immersed in water. Violent antiperistaltic waves may then be seen passing forward over the hood, and confined to that region of the animal (text-figs. 1*b–e*). After adhesion has taken place the animal usually begins normal locomotion, but sometimes on continued stimulation, a true leech-like movement takes place in which the hinder part of the body is brought forward towards the attached hood and the latter then re-extended.

It is evident that a structure capable of such movements requires a much more complex muscular organization than that of a simple sac-like muscular body wall. Sections show that the whole parenchyma in this region is traversed by a complex of muscle fibres. In the living animal, distinct appearance of a segmental organization can be seen, as in the extended hood of the animal shown in Pl. **2**, fig. 9, though it is difficult to trace any clear segmentation in the complex musculature seen in sections.

Discussion

The generalized effector systems of unsegmented worms can be utilized in various ways in locomotion. Like many nemertines, *G. dendyi* employs its ciliary field for normal locomotion. The muscular system is not directly used for ‘ gliding ’, but its potentialities are used in an interesting manner. In nemertines and planarians the muscular system is primarily a sac consisting of a muscular body wall enclosing a semi-fluid parenchyma with other tissues. Such a ‘ hydrostatic skeletal ’ system operates somewhat differently from the muscular systems of animals with jointed skeletons. A contraction at any point in the body wall has two distinct effects. It may directly cause a local movement of the body. This property is utilized in the lateral swaying movements of the head of *G. dendyi* and the Rhynchodemidae during photoklinotaxis. But any contraction also has the effect of raising the hydrostatic pressure in the parenchyma and thereby enforcing extension of the body at various points where the tone may be lower. This indirect effect of contraction is dramatically utilized in the eversion of the proboscis consequent on the synergic contraction of the circular musculature.

These properties of the hydrostatic skeletal system also allow the possibility of other effects which can be utilized for locomotion in various animals. In the planarians waves of muscular contraction are transmitted along the body wall and the direct and indirect consequences of these local contractions are utilized in different ways. *G. dendyi* does not use such muscular waves for locomotion, but many nemertines do so. Gray (1939) records how in a *Cerebratulus* freely suspended in sea water, waves of flexion pass down the body so that the animal swims after the fashion of a leech or flat-fish. On land, *Cerebratulus* like the majority of nemertines shows progression by the transmission of successive large peristaltic waves through its body. But whereas in the first case, swimming locomotion is primarily the direct result of local contractions causing the body surface to act directly on the surrounding medium, in the second the local swellings which constitute the large peristaltic waves seem to be the indirect result of local lowering of tone so that the internal pressure enforces a distension ; a condition similar to the ‘ myopodial ’ locomotion in *R. bilineatus*.

These examples of different locomotor mechanics in animals of simple and rather similar grades of construction are remarkably varied. Simple as are the effector systems they can be utilized singly or in combination in a variety of ways, and when locomotion is necessary in the behaviour pattern of an animal it may utilize any means at hand to accomplish it. This is less noticeable in the higher animals because we are accustomed to ascribe particular functions like locomotion to organs specifically developed for that purpose. But even in these cases an animal may sometimes ' cheat ' and use some wholly unexpected mechanism; as in a beetle of the genus *Stenus* (Billard and Bruyant, 1905) which moves over the surface of water by local lowering of the surface tension at the anus.

PART II. RHYNCHODEMUS BILINEATUS (*Mecznikow*) AND THE NAME OF FASCIOLA TERRESTRIS *O. F. Müller*.

In 1943 I found an unusual land planarian in woods round the Yealm estuary (Pantin, 1944). I have since found it abundantly throughout South Devon, and in woods at Fulbourn near Cambridge. I have also received a specimen collected by Dr. H. E. Quick from the Clyne valley near Swansea, Wales. Photographs of my living specimens which I sent to Dr. W. Adam were considered by him without hesitation to resemble worms taken by him near Brussels (Adam and Leloup, 1941) and identified as *R. bilineatus* (Mecznikow). Almost all previous records of this animal have been from continental greenhouses. The Belgian and British specimens were well established in the open. I shall discuss the distribution of these worms in a later paper.

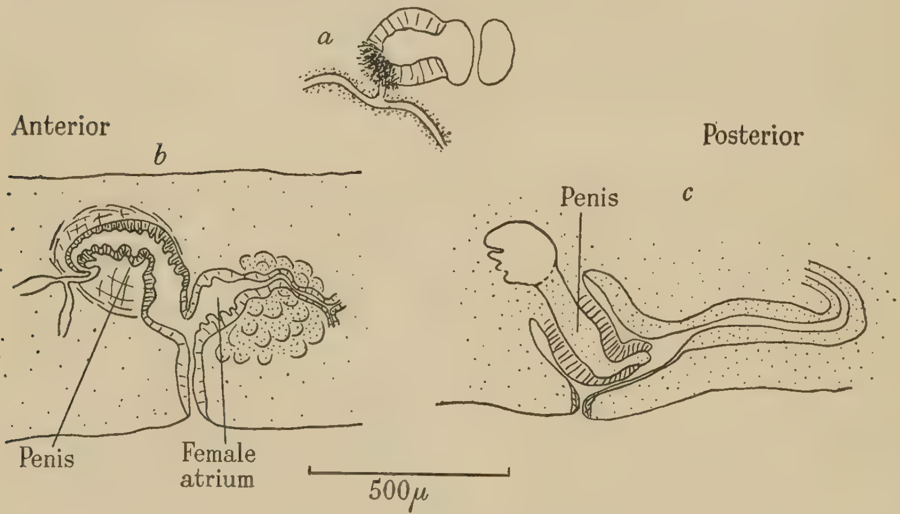

FIG. 4.

Head to left and tail to right in each figure.
a. R. bilineatus, living. Penis and pigmented vasa deferentia seen through dorsal surface. Genital orifice shown on right.
b. R. bilineatus. Reconstruction from sagittal sections of genitalia.
c. R. terrestris. Camera lucida drawing of sagittal section through genitalia. Contrast structure of penis with *b*.

Identity with Geodesmus bilineatus *Mecznikow.*

In my letter to *Nature* I noted the resemblance of my worms to Leidy's (1851 *a* and *b*) brief description of his North American *R. sylvaticus*. This resemblance still holds. But there is a more significant correspondence between my worms and *Rhynchodemus bilineatus*, as defined by von Graff (1899). This animal was described by Mecznikow (1866) with the name *Geodesmus bilineatus*. My animal agrees with Mecznikow's description in respect of general size, shape and colour, though I have found the range of colour to vary greatly from an overall dirty white with little trace of markings, through pale brown to purple brown to a dense brown black over the whole upper surface. The more significant resemblances concern: (1) The body is differentiated into an anterior flattened head (the cephalic hood) capable of rapid change of shape and in constant lateral movement, and a cylindrical posterior portion. This differentiation contrasts with the condition in *Rhynchodemus terrestris*. Pl. **2**, fig. 4 *b*, shows a specimen of the latter with its simple anterior end turned upwards. The difference from *R. bilineatus* in P. **2**, figs. 5–14, is striking. (2) The colour pattern is elaborate; the head is dark above and below, the body has two long dorsal stripes and a median dark saddle above the pharynx (Pl. **2**); the ventral surface of the belly is dirty white except for some half dozen brown spots joined by fine streaks of pigment (P. **2**, fig. 14). As Mecznikow figures, the spots are frequently circular. They are pigment deposited round the base of each testis and along the vasa deferentia. (3) There are large eyes just behind the snout. (4) The contracted penis, examined in compressed specimens can sometimes be seen to have the same appearance as that figured by Mecznikow; as in his specimens, the vasa deferentia join to a short common duct before entering the penis (text-fig. 4 *a*).

If we add to these characters, those noted by others (von Graff, 1899) in what they believed to be *R. bilineatus* we may note: (1) The specialized cephalic hood is grooved ventrally (Pl. **2**, fig. 9); (2) It is ribbed or segmented (Pl. **2**, fig. 11); (3) At rest it is turned upwards and backwards (Pl. **2**, figs. 13 and 14; also Lehnert, 1891); (4) Buck's (1897) excellent account of individuals from a German greenhouse leaves no doubt but that these animals were identical with mine, and includes a sketch of an animal in myopodial progression. All these characters contrast with those of *R. terrestris*.

There is only one point in Mecznikow's description of *R. bilineatus* which is hard to reconcile with my animals. He states that the animals are entirely covered with cilia, whereas in my specimens I have never seen any cilia except along the sharply localized and densely ciliated strip of the ventral creeping sole (text-fig. 2) the cilia of which are 5–6 μ long. In normal live and in anaesthetized animals, and in those well fixed in Susa or Formic-Zenker, no other external ciliation has been seen by me, though I have frequently been able to observe during life such fine ciliation as that of the nephridial canal system in both species. If cilia exist on the dorsal surface they must be exceedingly few and minute. The only other worker who offers evidence suggesting general ciliation is von Kennel (1882) who saw isolated cilia in teased shreds of tissue. But the possibility of these being derived from the creeping sole or from internal organs cannot be overlooked. It is possible that Mecznikow's original observation is subject to the same uncertainty. It is noteworthy that he did not detect that striking feature of the land Turbellaria, the ciliated sole, and that he states that the cilia were barely 2·5 μ long; the interpretation of such minute objects on the living tissues of a relatively large animal might present some difficulty even at the present day.

Notwithstanding this uncertainty concerning the extent of ciliation, the agreement of my animals both with Mecznikow's description and with the fuller descriptions by von Graff and others seems to leave no reasonable doubt that my animal is identical with Mecznikow's *Geodesmus bilineatus*.

Comparison of R. bilineatus (*Mecznikow*) *with* R. sylvaticus, *Leidy*.

Geodesmus bilineatus was subsequently referred to the genus *Rhynchodemus* along with *R. terrestris* and Leidy's *R. sylvaticus* (von Graff, 1899). Recently

Hyman (1943) has contrasted the anatomy of Leidy's *R. sylvaticus* with that of *R. terrestris* and other species. There are certain differences of considerable systematic importance. In *R. sylvaticus* the longitudinal body muscle is in conspicuous bundles, and the papilla of the penis is absent. In *R. terrestris* the longitudinal muscle of the body wall forms a relatively weak layer without bundles, and there is a large penis papilla (text-fig. 4*b*). Sections of my worms show well developed longitudinal muscle bundles (text-fig. 2*a*) and a penis without a papilla (text-fig. 4 *a*). They thus differ from *R. terrestris* and resemble *R. sylvaticus*. The whole genital system of my animals is strikingly like Hyman's figure of it in *R. sylvaticus*.

In addition to these internal characters, my animals possess general external features in common with Leidy's brief description and von Graff's summary of the characters of *R. sylvaticus*. The modified anterior part of the body (the cephalic hood) is flattened, with the edges inflected and with the tip recurved. At rest the head lies doubled upon the back. The colour pattern consists of two dark lines with a median spot. The eyes are large. All these characters would equally well fit Mecznikow's *Geodesmus bilineatus*. We may contrast them with the even cylindrical body of *R. terrestris* without a specialized cephalic hood (Pl. **2**, fig. 4) and the even dark colour or simple mottling of that species (Pl. **2**, figs. 1 and 4*a*) and the minuteness of the eyes.

From this it seems that my specimens are not only identical with *Geodesmus bilineatus* but also that they are closely related to *R. sylvaticus* Leidy (1851*a*). We are justified in considering them as congeneric. And since my animals appear to be *Geodesmus bilineatus* Mecznikow, 1866, it follows that they must be named *Rhynchodemus bilineatus* (Mecznikow), as von Graff named them for other reasons.

Systematic.

Several attempts have recently been made to clear up the somewhat confused systematic relations of von Graff's Rhynchodemidae (Heinzel, 1929; Hyman, 1943; Prudhoe, 1949). Unfortunately the fact that *Geodesmus bilineatus* appears to be a *Rhynchodemus* has serious consequences. Hyman (1943) has separated a sub-family with *Rhynchodemus sylvaticus* as the type. Its salient characters are the presence of longitudinal muscle bundles and the relative absence of a penis papilla. Since *Rhynchodemus terrestris* has no muscle bundles and has a well developed penis papilla it falls outside the sub-family and ceases to be a *Rhynchodemus*. *Rhynchodemus terrestris* is the original *Fasciola terrestris* O. F. Müller (1774) and is regarded by some as the type of the whole family : it is important that it should have a name. To supply a name Hyman turned to an anatomical paper by von Kennel (1882) from which she concluded that *Geodesmus bilineatus* Mecznikow has no muscle bundles and has a penis papilla, and that it therefore resembles *Rhynchodemus terrestris*, which can therefore become *Geodesmus terrestris*, within a sub-family Geodesminae. This anatomical interpretation is quite at variance with my observations on the anatomy of the animals I have here identified as Mecznikow's *Geodesmus bilineatus*. von Kennel and I may be describing two animals with some fundamentally different internal structures. But if so it is most remarkable that in all other characters both these animals not only show a detailed resemblance to Mecznikow's *Geodesmus bilineatus* but some resemblance to Leidy's *R. sylvaticus* and a direct contrast to *R. terrestris*. It seems desirable to consider whether von Kennel's account will bear the weight of the structure that must be erected upon it.

I suggest that Hyman's interpretation of von Kennel's account is open to doubt. His description of the muscular system is primarily a comparison of the condition in *R. terrestris* with aquatic Turbellaria. Though he occasionally makes a reference to *Geodesmus*, he gives no explicit description of its musculature and no comparison of it with that of *R. terrestris*. With regard to the genital organs, here again he gives no explicit description and comparison of the two species but rather a generalized comparison with aquatic Turbellaria. He gives however a stylized diagram of the condition in *Geodesmus* which certainly shows a penis papilla ; though this is smaller, and the penis sheath less developed, than in *R. terrestris*. The figure is stylized and may be influenced by what he saw in *R. terrestris*. It is significant that in this figure and in his account of the penis, von Kennel differs from Mecznikow, who believed that the penis of *Geodesmus* had quite a different structure ; and von Kennel also differs in stating that the vasa deferentia open directly into the penis and not by a common duct, such as Mecznikow figured, and such as I have found, and such as is also present in *R. sylvaticus*. Bearing in mind the malleability of the genital organs, the fact that von Kennel's attention was not directed to an explicit comparison of the two species, and the points of difference from Mecznikow's original, though limited, description, I do not think that von Kennel's account can overset the resemblances to which I have drawn attention between Mecznikow's *Geodesmus bilineatus* and Leidy's *R. sylvaticus*.

If it is admitted that *G. bilineatus* Mecznikow and *R. sylvaticus* Leidy are congeneric, the generic name *Geodesmus* becomes a synonym for *Rhynchodemus* and disappears. Müller's *Fasciola terrestris* cannot be given the generic name *Geodesmus* as suggested by Hyman. It must either be placed in the genus *Rhynchodemus* or its genus requires a new name. There seems no doubt from the work of Hyman (1943) that the differences between *sylvaticus* and *terrestris* are of at least generic magnitude and my present comparison of *bilineatus* with these species fully supports this conclusion. A new name is therefore needed for the genus containing *terrestris*. This is unfortunate since *terrestris* is regarded by some authors (e.g. Heinzel, 1929) as the type of the family Rhynchodemidae ; it being the oldest identifiable species ever assigned to the genus *Rhynchodemus*, though not the genotype, which is in fact *sylvaticus* Leidy (vide Hyman, 1943, and Prudhoe, 1949).

[Pending further comparison with other known species, it will create least confusion if we continue to follow von Graff and refer to *Rhynchodemus terrestris*, notwithstanding the fact that *terrestris* cannot be a *Rhynchodemus*.]

I wish to thank Dr. John Smart and Mr. S. Prudhoe for their most helpful criticism of this paper.

SUMMARY.

1. Normal locomotion in *Geonemertes dendyi* takes place by ciliary action. The animal secretes mucus over its whole surface and, though terrestrial, moves by swimming in this mucus, which is left as a trail behind it. The animal is negatively photoklinotactic ; the swaying lateral movements of the head responsible for this taxis are muscular. When suddenly stimulated the animal displays an escape reaction by using its proboscis. A simultaneous contraction of all the circular musculature causes its eversion. The animal then flies forward as a wave of longitudinal contraction and circular relaxation spreads up the body and proboscis.

2. Normal locomotion in *Rhynchodemus terrestris* takes place through muscular waves passing backwards down the ciliated muscular creeping sole of the ventral surface. A continuous mucus trail is left as the animal glides forward. The animal is photoklinotactic. In *R. bilineatus* these muscular waves are enormously exaggerated, and only touch the substratum at their lower surface. The animal thus moves by continually producing a succession of ' myopodia ' which develop in the neck region, protrude down to make contact with the substratum and then pass back along the ventral surface. The animal leaves a succession of isolated mucus foot-marks. Through the co-operation of muscular and ciliary action, the body surface continually glides forward where it is in contact with each foot-mark. This animal also is negatively photoklinotactic.

3. *R. terrestris* on occasion may show large leech-like locomotor movements due to powerful antiperistaltic waves in the hinder part of the body. *R. bilineatus* has a specialized muscular cephalic hood. This may on occasion be used as an anterior sucker in leech-like progression with alternate longitudinal contraction and extension.

4. The varied ways in which these comparatively simple ciliary and muscular effector systems are utilized for progression are discussed. An animal may develop any convenient property of its effector system to meet the locomotor requirements of its behaviour pattern. At times it may ' cheat ', as in beetles that swim by local lowering of the surface tension.

5. The occurrence of a land planarian new to Britain is recorded. It is identified as *Geodesmus bilineatus* Mecznikow=*Rhynchodemus bilineatus* (Mecznikow). Its resemblance extends to internal structure.

6. *R. bilineatus* is congeneric with *R. sylvaticus* Leidy. Both are generically distinct from *Rhynchodemus terrestris* O. F. Müller. The latter should not remain named either *Rhynchodemus terrestris* or *Geodesmus terrestris* as it has been by some recent authors. It requires a new generic name.

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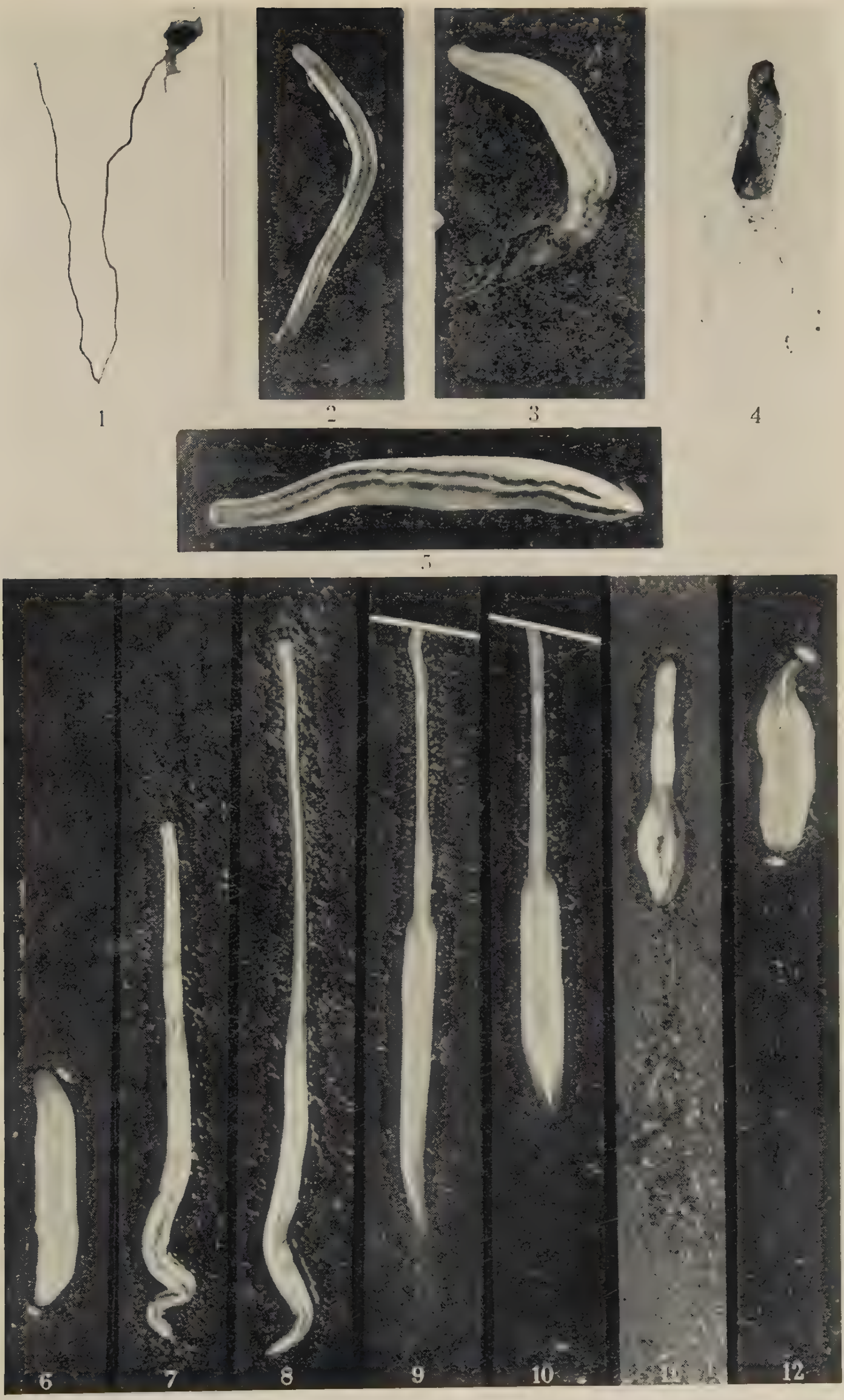
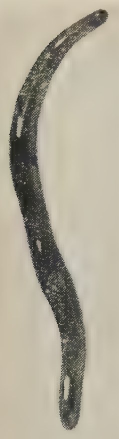


Geonemertes dendyi.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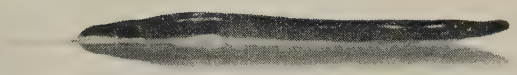
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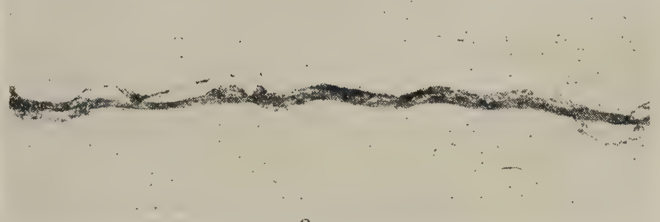
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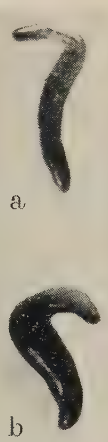

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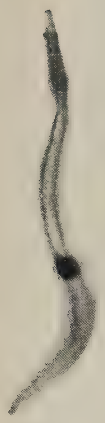
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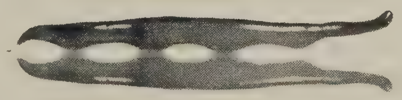
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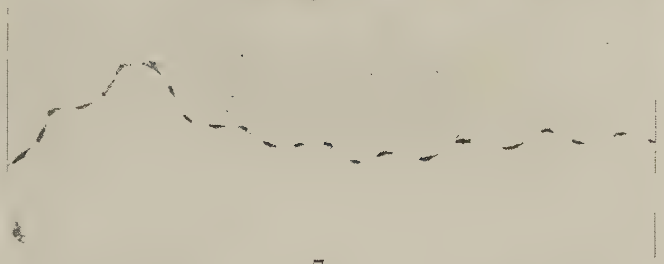
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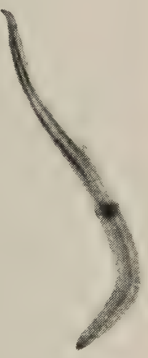
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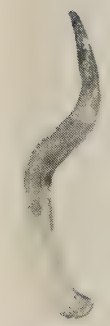
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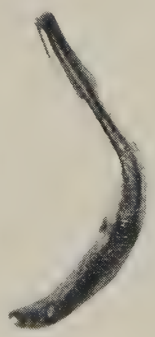
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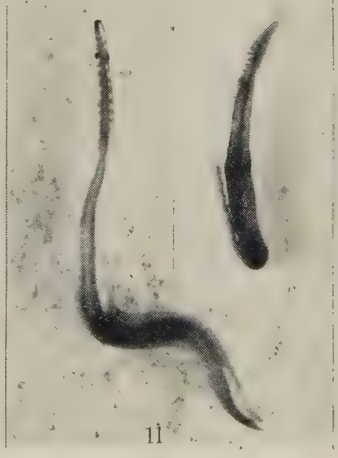
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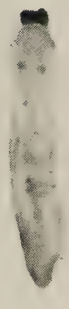
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EXPLANATION OF THE PLATES.

PLATE 1.

Geonemertes dendyi.

FIG. 1.—Mucus trail. (× 2/3.)
FIG. 2 (× 2) and FIG. 5 (× 7).—Normal locomotion.
FIG. 3.—Escape from slime cocoon. (× 7.)
FIG. 4.—Slime cocoon. (× 3.)
FIGS. 6 to 12.—Eversion of proboscis and flight reaction. (× 5.)
(For further explanation see text.)

PLATE 2.

FIGS. 1–4.—*Rhynchodemus terrestris.*

FIG. 1.—Normal view. (× 6.)
FIG. 2.—Lateral view in locomotion. (× 4.)
FIG. 3.—Mucus trail. (× 3.)
FIG. 4.—Two young specimens, (*a*) with mottled pigmentation, (*b*) exposing anterior ventral surface. (× 6.)

FIGS. 5–14.—*Rhynchodemus bilineatus.*

FIG. 5.—Normal view. (× 8.)
FIG. 6.—Lateral view in locomotion. (× 6.)
FIG. 7.—Mucus trail. (× 3.)
FIG. 8 (× 6), FIG. 9 (× 6), FIG. 10 (× 8) and FIG. 11 (× 8).—Show different shapes assumed by cephalic hood.
FIG. 12.—Swaying of head when locomotion starts. (× 6.)
FIG. 13 (× 8) and FIG. 14 (× 10).—Resting animals.
FIGS. 9 and 14 are ventral views.

PROCEEDINGS OF THE GENERAL MEETING ON 9 February 1950

Colonel F. C. STERN, O.B.E., M.C., Vice-President, in the Chair.

The Proceedings of the General Meeting held on Thursday, 19 January 1950, having been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Professor A. J. E. Cave, Dr. S. E. Chandler, O.B.E., Mr. Earle A. Davison, Professor Ralph Dennell, Dr. E. A. Fraser, Dr. I. Gordon, Mr. P. S. Green, Mr. Cecil H. Hooper, Mr. N. B. Kinnear, C.B., Professor F. J. Lewis, Dr. L. Harrison Matthews, Mr. T. C. S. Morrison-Scott, D.S.C., Mr. J. R. H. Nash-Wortham, Mrs. W. H. Oldaker, Dr. G. S. Puri, Dr. Alfredo Ramaldo, F.M.L.S., Mr. F. Rilstone, Dr. T. A. Sprague, Col. F. C. Stern, O.B.E., M.C., Mr. W. L. Sumner, Professor D. A. Webb, Professor F. E. Weiss, F.R.S., Dr. Errol I. White, Mr. W. C. Worsdell, Carnegie Institution of Washington and the British Society for the History of Science.

The following Fellow signed the Obligation in the Roll and Charter Book, and was admitted a Fellow :—Mr. Henry Idris Matthews, O.B.E., M.C., B.Sc.

The Vice-President in the Chair reported the death of Alfred James Wilmott, M.A., Fellow of the Society.

A DISCUSSION ON SUCCULENT PLANTS was opened by Dr. E. M. DELF, Prof. T. A. BENNET-CLARK and Mrs. VERA HIGGINS, V.M.H.

In the general discussion the following took part :—The Vice-President in the Chair, Dr. W. B. Turrill, Sir Nigel G. Ball, Bt., Dr. A. C. Halket, Major Patrick M. Synge, Mr. A. H. G. Alston, Prof. G. D. Hale Carpenter, M.B.E., Mr. F. C. Grigg ; Dr. Delf, Prof. Bennet-Clark and Mrs. Higgins replied.

The following papers were read in title :—

'Note on a Skull of Hector's Beaked Whale *Mesoplodon hectori* (Gray) from the Falkland Islands'. By F. C. FRASER, D.Sc., F.L.S.

'Abnormalities in the Sexual Apparatus of the Common Dogfish (*Scyliorhinus caniculus*)'. By D. R. ARTHUR. (Communicated by Dr. S. M. MANTON, F.R.S., F.L.S.)

'The homology of the Mammalian Pterygoid in the light of some new evidence'. By F. C. ELOFF, D.Sc. (Communicated by Prof. G. R. DE BEER, F.R.S., F.L.S.)

'Occurrence of *Lysiosquilla scabricauda* (Lamarck) in Bermuda'. By Prof. RALPH DENNELL, F.L.S.

A DISCUSSION ON SUCCULENT PLANTS

BIOLOGICAL FEATURES OF SUCCULENT PLANTS

By Dr. E. M. DELF.

(With 2 Text-figures.)

Succulent plants appear to be popular today, not only with the grower, but also in the laboratory. Their peculiar appearance and habit make them of interest to the former, but they also have a special interest for the physiologist in connection with their water economy and for the biochemist in connection with their metabolic processes. Each of these aspects will be considered, at least to some extent in the discussion to-night.

We must first ask, what are succulent plants ? In general terms they may be said to be plants with a marked capacity for the accumulation and retention of water, or more briefly, for water storage. For what purpose (if any) and by what means the storage is effected are rather different questions about which opinion is divided.

A good many years ago, seeking for a more definite criterion, I suggested that succulence might be roughly estimated in terms of water content per unit of assimilating surface (Delf, 1912). I still think this a useful criterion ; but it is not easy to estimate the surface areas of some plants, and Evenari, in a paper before this Society (1937) defined as succulent those plants which had a high ratio of water content to dry weight. However, the succulent plant has also certain biological features associated with the water storage. These are mainly related to their water economy, their metabolism and their capacity for regeneration ; it will be seen that these features although distinctive are by no means uniform throughout the group.

Specialized Habitats.

Most of these plants thrive in places with bright natural illumination, frequently in dry stony soil with an intermittent and more or less scanty rainfall; they may form, however, but a small part of the total vegetation present. This is noteworthy in the S. African Karroo, for example, and Sabnis (1920) found that of 20 genera from 15 different families in the Indian desert of Rajputana, only 9 had water storage and could be regarded as succulent. Examples of such specialized localities are :—

N. America (Arizona)	Cactaceae,	*Cereus*, *Opuntia*, etc.
	Euphorbiaceae,	*Euphorbia* spp.
S. Africa (Karroo)	Liliaceae,	*Aloe* spp.
	Aizoaceae,	*Mesembryanthemum* spp.
	Euphorbiaceae,	*Euphorbia* spp.
	Asclepiadaceae,	*Stapelia* spp.
Europe (High Alps)	Crassulaceae,	*Sedum* spp., *Sempervivum*, etc.

Although these plants are characteristic of habitats with both edaphic and atmospheric dryness they can be grown fairly successfully in our climate, with its frequent damp and sunless days. It is this combination of specialization and adaptability which makes them of such interest to the biologist.

Succulent plants are also found in wet saline areas, such as maritime salt-marshes and the ' solfataras ' of the continent. Unlike the succulents of dry places, these are found in humid conditions. They are mostly representative of the great family of the Chenopodiaceae ; in this country *Salicornia* and *Suaeda* are familiar examples.

Whilst the Cactaceae (and probably also the Euphorbiaceae) have a low transpiration rate and high resistance to water loss, Evenari (1937, p. 17) found that *Suaeda asphaltica* of the Judaean " Wilderness ", with succulent leaves had a low transpiration rate and little resistance to dry periods ; but he noted that the leaves are deciduous. On the other hand, *Salicornia* and *Mesembryanthemum* (especially *M. crystallinum*, Delf, 1912), have a transpiration rate equal to or higher than that of many mesophytes, and have little capacity for resistance to deprivation of water.

Stem and Leaf Succulents.

Although there are some plants which store water in their roots or underground organs, the commoner plan is for stored water to occur in the ground tissue of the stem or leaf. *Stem succulents* usually have great reduction of leaf surface, the swollen stems taking on what appear to us as bizarre shapes. They are typically shallow-rooted, the rootlets widespread, with power of rapid absorption in the short rainy periods ; the stems swollen and cylindrical (or even orbicular) when replete with water, becoming fluted with water deficit. The grooves of the sunken regions doubtless protect the stomata to some extent both from direct illumination and from the full effects of a dry atmosphere.

Stem succulents are well represented by the Cactaceae and the Euphorbiaceae; these have a low transpiration rate (as far as observed) even when water is available and also a remarkable power of survival in the prolonged absence of water. In the latter condition, the older parts are gradually sacrificed to the younger which retain the power to resume growth on restoration to favourable circumstances. Mucilages, resins and organic acids are characteristic cell inclusions and may play their part in this long persistent vitality.

However, it should be noted that not all stem succulents have this capacity. The leafless swollen stems of *Stapelia squarrosum* for instance lived only two weeks (Tab. I) when deprived of water, although quite as succulent as the more resistant types. Physiologically there must be great differences in these stem succulents, in spite of their somewhat similar external modifications.

Leaf succulents are less sharply defined morphologically, but the fleshy leaves have a range of physiological characters similar to those of the stem succulents. Many species of *Aloe* have the habit of small trees with fleshy leaves crowded towards the ends of their branches ; other types are herbaceous like the Mesembryanthemums. Some species of *Mesembryanthemum* have long pendulous branches (e.g. *M. edule*) others only have two or four sessile leaves, appressed and so swollen as to form a sphere (e.g. *M. auranticum*). The former species has a high rate of water loss, and some power also of sacrificing old leaves for the supply of water to the young ones during deprivation of water (Delf, 1912). Few species of *Mesembryanthemum* have been tested, but *M. Forskalei* has also a rapid transpiration rate according to Said and Tolba (1948). In the Crassulaceae, the genus *Sedum* (Delf, 1912) and *Kalanchoë* (Migahid, 1937 ; Said and Tolba, 1948) have also a relatively high transpiration rate ; in many Crassulaceae there is a marked power of regeneration, whether from adventitious buds or from detached shoots which survive for a longer or shorter time without water, the meristems being supplied from the older leaves with water and, doubtless, also with other substances.

The giant Senecios of the high mountains of Central Africa have very succulent leaves and would be of great interest in this connection, for they live on slopes at high altitudes where the atmosphere is often saturated with water vapour, and where there are also extremes of temperature, high by day and intensely cold at night (Cotton, 1930, 1932 ; Leighton Hare, 1941). The anatomy shows that the leaves are hairy, with a great development of water storing tissue and that the epidermis is thin-walled, but we have no obvious explanation (and no available evidence) to show how this water-storing tissue functions. Similarly, the rôle of the watery sap in the densely packed succulent and hairy leaves of the desert species of *Anabasis* is purely conjectural.

Water Economy of Succulents.

It is well known that many succulent plants can survive without water for long periods. A rough idea of the endurance can be obtained by hanging up cut shoots (the cut ends being first sealed) to dry in ordinary air. By weighing the shoots initially, from time to time and after drying at 100° C, the progressive loss in weight can be calculated in terms of the initial water content. Naturally, shoots are chosen which do not show signs of water deficit at the start.

The diagram (fig. 1) shows typical results of such an experiment made in the winter of 1942, in a very chilly laboratory and for the most part in cold weather. It will be seen that the three types, *Aloe, Opuntia* and *Phyllocactus* had a low rate of water loss from the first ; they lived for more than seven months, the lower parts drying slowly back, but the apical regions persisting without loss of vitality. The segment of *Opuntia* was kept in this way for more than a year, when only 1–2 cm. of green tissue remained ; but on access of moisture, it developed successfully into a small plant. On the other hand, the shoots of *Stapelia* and *Cotyledon* lost their water rapidly and soon died. In *Stapelia* this seemed to be a general collapse with no conservation of water supply in favour of the young tissues.

The question of endurance has been further studied in the *Aloe* (*A. arborescens*). Here, as the shoots dry, the lower leaves become concave upwards, their toothed margins approaching each other or even interlocking. As each leaf dries, the next above begins to show signs of water deficit, but the upper leaves remain for long unchanged. Two shoots, D1, D2 were kept without water for eight months, after which both were reduced to skeletons bearing each two small green leaves, the inner tightly rolled around a still smaller leaf

TABLE I.—Endurance of Water Loss in cut shoots of Succulents.

			Water content %
Opuntia	7 months	Upper regions still alive	82–89
Phyllocactus			89
Aloe			90–95
Bryophyllum			79
Cotyledon	3–4 weeks	Dead	80
Stapelia	2–3 weeks	Dead	96
Polygonum	5–10 days	Dead	—

rudiment not 1 cm. in length. D2 had seven green leaves originally; it resumed growth and recovered completely after having access to water. D1 had nine green leaves originally; it was kept without water for a further period. During the next six months, the outer leaf withered completely, and the next inner for about a quarter of its length. In the last five months, this leaf was also emptied and only the small rudiment (2 cm. in length) remained green. It may be seen on the table to-night, still erect on its now papery shoot, but showing signs of flaccidity (fig. 2).*

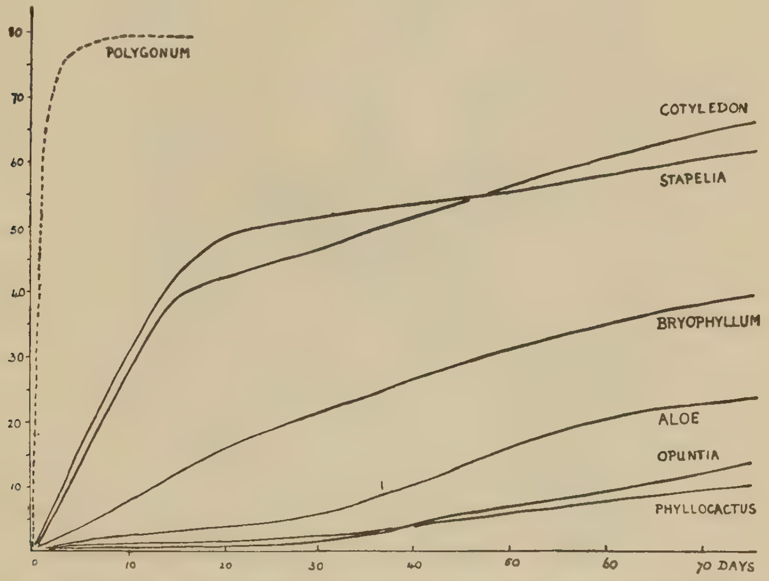

FIG. 1.—Progressive loss in weight of detached shoots drying under laboratory conditions. (Plotted as % of fresh weight.) Nov.–June 1922–3.

Examination of such a dried stem shows that the cells of the ground tissue are empty and torn, where previously they would have been filled with needle crystals or with solid matter which swells readily on contact with water. It would appear that these cell contents play an important part in maintenance of the life of the shoot. Even after the cells of the ground tissue are empty, the meristematic cells of the cambiform region remain turgid, and may even give rise to small adventitious shoots, or, if near the cut end, to a ring of short, hard, adventitious rootlets which elongate quickly if reaching water. This appears to be quite a different thing physiologically from the persistence of the hard shoots or leaves of certain sclerophyllous plants, such as the S. African *Passerina*, the leaves of which go into a sort of anabiosis with loss of water (Thoday, 1921). Here the air-dry cells swell again with absorption of water and resume their normal activities.

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* On the following day, 2–3 cm. of stem were removed and the new surface allowed to touch sterile rainwater. Within a week the base of the leaf seemed more translucent; in another two weeks the rudiment had gained about 2 mm. in length, had widened and the apex of a new leaf rudiment was clearly visible. Thus growth had been resumed.

Progressive Starvation in Water.

The capacity to do without water does not necessarily imply that available water cannot be utilized. The shoots of *Aloe* form roots fairly easily from the cut ends, and the roots can absorb water freely for a long time, provided only that the stem itself is not submerged, when a black rot is liable to appear. Two such shoots have been kept in sterile rainwater for 2½ years. There is no sign of water deficit in any of the leaves while still green, but the lower leaves dry out from the apex backwards, with an abrupt transition from the thick turgid lower part to the dry distal region of the leaf. New leaves form slowly from the apex, but their size becomes progressively less. After 2½ years the total number of leaves has only slightly diminished, but the original leaves have been replaced by others less than half their size, presumably owing to mineral starvation. In the light of these observations, it is not surprising that these aloes can thrive in very poor soil and in the presence or absence of water within wide limits, provided only that the soil itself is not water-logged.

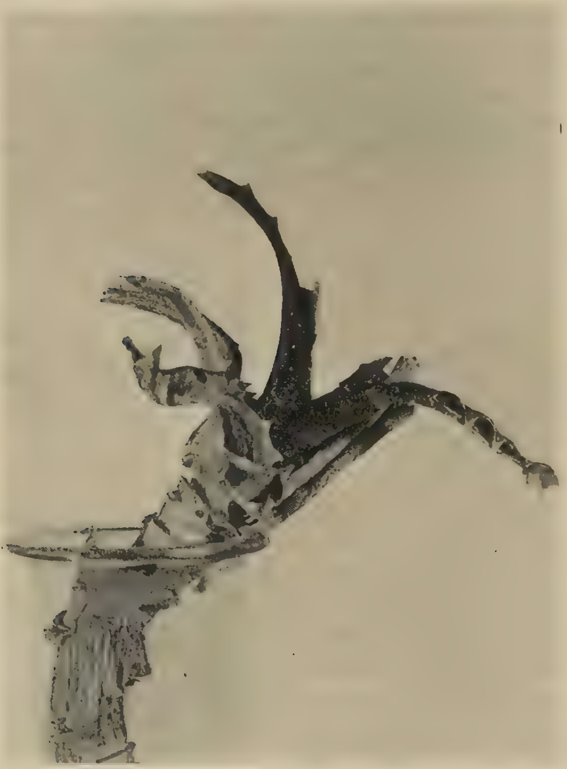

Fig. 2.—Photograph showing close-up of D1 after more than 14 months of desiccation. The intact leaf is about 3½ cm. in length, the rudiment within it about 0·7 cm. long.

Nutritive solutions.

Similar plants can also be successfully grown in culture solutions. Indeed all my plants originated from the cutting given in 1917 to Dr. L. J. Clarke at the James Allen's Girls' School, Dulwich. When given water, the cutting developed adventitious rootlets which were then placed in a Sach's culture solution, renewed at roughly monthly intervals. I was informed by her successor, Miss E. Fogg, that it survived for twenty-three years, dying in 1940 during a very cold spell when, owing to fuel shortage, the laboratory in which it was kept was left unheated over the week-end.

This plant had branched freely and from time to time basal shoots were removed, cultured separately and duly recorded. One of these, removed in 1929, was given to me six years later. It was transferred soon after to a large pot where it thrived until last year, dying in 1949 from rot engendered during a hot spell in a greenhouse which was underventilated and over-watered in the absence of the staff and of the usual gardener. I should like here to pay a tribute to the remarkable feat performed by Dr. Clarke and her successors in keeping steady records of these plants and in maintaining the care of them for so long, with the minimum of assistance and in the midst of the many other claims on their time.

Stomata.

It is sometimes said that the stomata of succulent plants close by day and open by night, as found by Macdougall for the Cactaceae. So far as I have seen, this is not the case for the following: *Opuntia, Salicornia, Sedum acre* and *Mesembryanthemum edule,* Migahid found active stomatal movement in *Kalanchoë aegyptiaca* (1937), while Said and Tolba reported the same in *Mesembryanthemum forskalei* and *Kalanchoë marmorata* (1948). In recent observations, experimental plants of *Aloe* had mostly closed stomata, others being narrowly open. The lack of widely open stomata was not however surprising for the observations were made during cold and rather dull winter weather. As stomatal movement is determined to a large extent by the interaction of light, temperature and internal (or epidermal) water content, negative results do not necessarily imply any fundamental peculiarity.

Many other problems arise in connection with the water economy of aloes which cannot be included tonight. . . such as the question of the conducting capacity of the vascular tissues, the influence of ions on water movements, the susceptibility to black rot (apparently connected with faulty aeration). However, enough has probably been said to show the wide range of the biological characteristics of succulent plants and the remarkable differences in their water economy, so far as this has been ascertained.

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SPECIALIZED PHYSIOLOGY AND BIOCHEMISTRY OF SUCCULENT PLANTS

By Prof. T. A. Bennet-Clark.

Discussion of the specialized physiology and biochemistry of succulent plants must bulk large in a symposium on such plants and the rôle of this paper is to deal with their biochemistry since the water relations have been considered by Dr. Delf.

Succulent plants are found in many widely distinct natural orders both monocotyledonous and dictoyledonous, and, so far as is known, most of them show somewhat similar physiological behaviour though admittedly very few species have been intensively studied. If one excludes halophyte succulents, it is probably true to state that succulents are among the very few xeromorphic plants in which transpiration per unit area is lower than it is in mesophytic plants under conditions of good water supply and illumination.

Their biochemical peculiarities may be associated with this physiological habit. This special feature is their capacity to become acid during the night and to lose this acidity during the subsequent day. It has been said that this sort of behaviour was known to the younger Pliny who noticed the increased acidity of salad plants collected in the morning, but the first scientific study was by Robert Mayer who determined approximately the course of the diurnal fluctuation by titration and who also attempted an identification of the acid produced. His analyses led him to suppose that it was malic acid but as it differed from normal malic acid he thought it was an isomer and later another chemist termed it ' crassulaic malic acid '. Since no isomer is possible this view was curious and it is only during the last decade that the difficulty has been resolved ; Pucher and Vickery have shown that the acid present is a mixture of relatively large amounts of *iso*citric and malic acids together with much smaller quantities of citric and traces of other related acids.

The diurnal fluctuation in acidity is due almost entirely to change in quantity of L-malic acid and this change is associated with a fluctuation in carbohydrate content in the opposite sense (*i.e.* maximum carbohydrate coincident with minimum acidity).

Non-succulent plants when darkened respire taking in oxygen and producing carbon dioxide which one regards as ' normal '. Extreme succulents have for some time been known to behave differently. On darkening, oxygen is absorbed relatively quickly but the rate of carbon dioxide output falls to a very low value and may cease completely. Recently Thomas (1949) has shown that carbon dioxide is under certain conditions actually taken in in darkness and during this process organic acid (known from other work to be L-malic acid) accumulates.

Miss Wood similarly has shown that during this phase the quantity of malic acid formerly is more than 1 mol per mol of glucose lost from the form of starch and that it frequently approaches 2 mols/mol glucose, so that a gain or uptake of carbon must have occurred.

Bonner and Brown (1949) have shown also that CO_2 is an active agent in promoting acid formation. It was noted that in certain succulents, especially *Bryophyllum fedtschenkoi*, the plants are very sensitive to changes in CO_2 content in the concentration range from 0–0·03%.

Those are the main facts. Whereas a normal plant in respiration takes in oxygen and gives off carbon dioxide, an extreme succulent at the phase when it has plenty of carbohydrate in its tissues either takes in CO_2 and produces malic acid or produces this acid with a small intake of oxygen.

$$2C_6H_{12}O_6+4CO_2 \rightarrow 4C_4H_6O_5,$$
$$2C_6H_{12}O_6+3O_2 \rightarrow 3C_4H_6O_5+3H_2O.$$

One should perhaps explain that respiration which provides energy for the plant's needs uses a source of fuel—largely starch in many succulents. Energy-yielding fuel is of no service without a suitable machine to be driven and the nature of the machine in living tissues is still distinctly uncertain. Two mechanisms have suggested themselves; the first involves oxidation of a type of phosphate ester termed a carbonyl-phosphate formed by addition of phosphoric acid to an aldehyde:

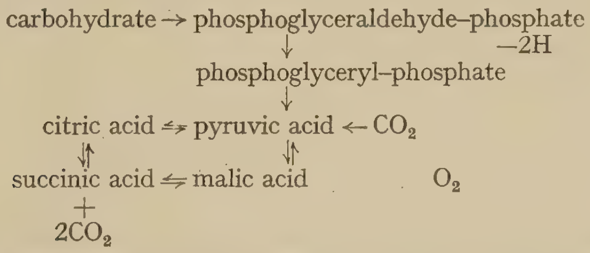
$$\mathrm{RCHO} + \mathrm{H_3PO_4} \rightarrow \mathrm{R\,.\,CH^*(OH^*)(OPO_3H_2)}.$$

The starred hydrogen atoms are removable by an enzyme system (a dehydrogenase) with formation of a substance $\mathrm{R\,.\,CO \sim (OPO_3H_2)}$. Now the free energy associated with the bond between phosphate and the rest of the molecule is greater in the compound $\mathrm{R\,.\,CO \sim (OPO_3H_2)}$ than in $\mathrm{R\,.\,CH(OH)\,.\,(OPO_3H_2)}$ and in most organic phosphate esters and is written with the symbol $\sim$ to indicate the presence of the high energy phosphate bond.

This type of compound can be used to form phosphate esters of sugars etc. which by reason of their energy level can be used for synthesis of polysaccharides and other substances. The formation of active phosphate bonds involves removal of pairs of hydrogen atoms and transfer of these to other substances. The organic acids play an important rôle in bringing this process about.

A second type of machine which is being thought about at present also involves a continuous supply of H atoms or perhaps more accurately electrons to a part of the living system that can perhaps be likened to a metallic wire which may conduct electrons from where they are supplied—possibly by the organic acids—to a region where they are taken up by reaction with oxygen of the air. Such a flow of electrons, constituting a bio-electric current, may be a mechanism by which salts and other substances are secreted by tissues.

The actual oxidations (or dehydrogenations) are thought to be concerned with the organic acids which probably are involved in cyclic reactions such as:



The four acids are linked in a cyclic series of reactions which going clockwise takes up the hydrogen removed from the phosphoglyceraldehyde phosphate. What is significant is that there are at least two pathways for removal of these 2H. One is an eventual transfer to the oxygen of the air, the other which is of great importance to succulents is a transfer resulting in formation of malic acid. This malate formation requires a supply of carbon dioxide.

The special peculiarity of the succulent seems to be that it is so constituted that the rate of formation of malate exceeds that of its decomposition which causes malate to accumulate with consequent uptake of hydrogen. Thus a type of respiration can occur in which loss of carbon to the outside world does not occur appreciably and the water supply problems associated with necessity for open stomata and easy gas exchange in photosynthesis are possibly much less acute than in more normal xerophytes. Both gas and water vapour exchanges of succulents are markedly slow.

In this brief account, many aspects have been treated as more certainly known than is in fact the case. There are many loose ends in the tissue of hypotheses. Striking fluctuations occur in the L-malate content of succulent plants with little or no change in *iso*citric content ; why this should be is a major theoretical difficulty and there are many others, of which the most incomprehensible is the absence of acid accumulation from carbohydrate under anaerobic conditions.

One has however in succulents plants a most valuable research material since one can obtain tissue of such strikingly varied carbohydrate and acid contents, and this should assist one in analysing the mechanisms which are involved in a range of life processes such as salt and water absorption, growth and other activities.

SUCCULENT PLANTS UNDER CULTIVATION

By Vera Higgins.

Herbarium specimens are like the index to a book—essential but dull ; the living plant is the reading matter, from which more can be learned, especially in the case of succulent plants, many of which differ markedly in the growing and in the resting period. It is not always possible for the botanist to visit the habitats of the plants with which he has to deal, and the collector is often in the field for a few days or weeks only. But, if living material is collected, it is possible for it to be cultivated so that the plants can be studied, not only as found, but through their annual cycle of growth.

Contrary to popular belief succulent plants do not occur in very arid deserts, which have as a rule a xerophytic flora only, but in semi-deserts where there a certain amount of moisture at some period of the year. Thus there are no succulent plants native to the Sahara, the Gobi Desert or the vast desert areas of Australia. The family Cactaceae, which is entirely American in origin, is found in that continent from Alaska to Patagonia, but is developed (apart from the epiphytic types found in the forests of Central America) in the warmer deserts of relatively high rainfall. The most interesting and varied succulent flora in the world is found in South Africa, again in the semi-desert regions.

To have succulent plants from different countries growing together can be very illuminating, and their behaviour shows that it is unwise to generalize. For instance, Cacti, whether they come from the deserts of North or of South America, can all be rested in this country during our winter and grown in our summer. But succulent plants from South Africa are reluctant to change their season and many of them, summer growers in South Africa, prefer to grow here during the same period of the year, which is our winter—a difficult time to give them the conditions they need, because of the absence of strong sunlight.

The flora of South Africa includes both stem and leaf succulents, the degree of succulence in the latter varying from leaves which are only slightly thickened and borne on woody stems to the extreme types which consist of only one pair of leaves, these being without stalks and often hemispherical in shape. The most extreme of all are the Lithops and Conophytums, where the whole plant is a little top-shaped body composed of two leaves fused together except for a slit along the upper surface.

Plants which show moderate succulence can be grown with no definite resting period, though naturally they remain truer to type if water is withheld for a period, preferably at their normal period of dormancy. But the resting period has to be more precise the greater the degree of succulence ; Lithops and Conophytums must have a period of complete rest during which the younger pair of leaves grows within the older pair which shrivels or, in the case of Conophytums, dries to a papery skin. In such genera as *Argyroderma* and *Pleiospilos*, where the plant consists of one pair of hemispherical leaves with their faces together, the new growth appears between them pushing them apart. If water is given continuously, two or more pairs of fully grown leaves may be present simultaneously, but if water is withheld at the proper time, the young leaves will draw on the reserves in the old leaves for the completion of growth.

It is also found that some succulents will start into growth after the resting period *before* the soil in which they are growing is watered, whilst others make no move until the soil has been moistened again. Xerophytes seem definitely to need the stimulus of water at the roots ; for instance, a plant of *Fouquiera splendens* which had put out a crop of leaves annually for some fifteen years, failed to do so in the succeeding two years, although it had had light overhead watering. A cut across the tip of a branch showed that the wood was still green, so the pot was soaked in water for two days and in less than a week the stems were covered with small green leaves ; the soil had become quite dry and overhead watering was not sufficient to induce growth.

Plants with large storage organs which make an annual growth of succulent leaves may be considered as intermediate between xerophytes and true succulents ; they may or may not need moisture at the roots to induce the renewal of the growing season. But extreme succulents, such as Mesembryanthemums, will usually, in cultivation, find enough moisture in the air to start them into growth after a rest of four or five months, even if the soil is quite dried out. And this suggests that succulent plants may make considerable use of dew, and that the rainfall records for an area do not necessarily give a true picture of the amount of moisture available. For instance, the western coast of South Africa has a very low rainfall ; Dr. Harry Bolus (1905) records that the mean rainfall over a period of ten years was 6·24 inches at Vanrhynsdorp, and only 2·45 inches at Port Nolloth ; but he adds : " the whole coast in this part is subject to frequent fogs which probably would not condense into a rain gauge, but would collect upon the vegetation. When I visited Port Nolloth in August, and again in September 1883, I found the atmosphere very humid, although there was no rain ".

Livingstone (1907) and Edith Shreve (1916) found that succulent plants transpire more freely at night than in the day-time and, since the intensity of transpiration is roughly proportional to the rate of absorption, this would suggest that they take in water at night mainly, that is, at the time when the drop in temperature causes dew fall. Though the root systems of xerophytes tend to go very deep, especially if there is a water table that can be reached, those of succulent plants are normally extensive in lateral directions and, even for quite small plants, may run for several yards ; but they are rarely more than two or three inches below the surface of the soil, a position in which they would be able to make use of slight showers or heavy dew.

In any case it is hardly likely that all succulent plants will behave in the same way, for the succulent habit, which has been induced as a response to environment, is superimposed on the characteristics of the family to which the plant belongs. Thus Cacti and Euphorbias may bear a very marked superficial resemblance but, whereas Euphorbias have firm flesh and abundant latex, Cacti usually have a much greater development of parenchyma and seldom have latex.

Much of the experimental work on succulent plants has been carried out on Cacti, chiefly at the Desert Botanical Laboratory at Tucson, Arizona, by Macdougal, Spalding, Forrest Shreve and others. Maximov (1929) uses, as examples of succulent plants, species of *Zygophyllum* and *Sedum*, but the extreme types of *Mesembryanthemum*, such as *Lithops* and *Conophytum*, do not seem to have been so extensively studied in the laboratory, and whether all types of succulent plant have the same physiological reactions seems to me doubtful. After some twenty years the collection under observation now includes representatives of 19 families and about 150 genera, and they certainly cannot all be treated in the same way even allowing for the differences in the season. Maximov suggests that succulent plants are ' drought enduring ' and that they will grow better in moister conditions, giving as an instance the fine collection of Cacti at the Buitenzorg Gardens in Java where the conditions are very warm and humid. The Cactaceae are certainly adaptable and, if difficult to grow true to type in this country, are also difficult to kill; but some of the South African succulents are much less adaptable and quickly succumb to excess water.

Besides the physiological problems that can be investigated from live material, there are also taxonomic problems which may need reference to the living plant. In his preface to the sixth volume of *Flora Capensis* Thistleton Dyer says: 'The advantage of consulting living specimens is of peculiar importance in describing the Petaloid Monocotyledons. But in the case of the succulent genera, it may safely be said, that, without it, the task would not be possible at all'. The preparation of dry herbarium material from fleshy specimens is rarely satisfactory; preservation in spirit has advantages but requires a large amount of storage space. The growing of specimens under proper conditions gives the botanist the best opportunity of examining the plant, not only on arrival, but throughout a year's growth. It is important that succulent plants should be grown as true to type as possible, and the conditions required are now much better understood than formerly.

When plants first came from the Cape in the latter part of the eighteenth century and for some time after, it was thought that they needed a hot, humid atmosphere; many of the early illustrations, beautiful as they are, show that the specimens from which they were drawn had been grown too soft, with consequent lengthening of the internodes and so forth. One of the worst examples that I have come on is the original description of *Crassula Cooperi* by Regel in *Gartenflora* (1874, p. 36, t. 786); in the accompanying illustration it is shown as a weak-stemmed, straggly plant hanging down all round the pot. About the same time, in the *Botanical Magazine* (t. 6194) Hooker described *Crassula Bolusii* from plants in cultivation and the plate shows a similar weak-stemmed plant, in fact he says: 'As a species it is closely allied to *Cr. Cooperi* Regel . . . but differs in the less straggling habit', which probably means that the Royal Botanic Gardens grew the plant better than Haage and Schmidt of Erfurt, who produced Regel's specimen. In nature this *Crassula* makes compact mats about an inch high, and there is still much discussion as to whether the two descriptions do or do not refer to the same plant.

Succulents show evidence that, as a class, they have not reached a position of equilibrium but are still actively evolving. With regard to the Cactaceae, Forrest Shreve (1931) says: 'A great many Cacti have areas of distribution which are very small and nearly all of them are limited to much smaller regions than is generally the case with species of other flowering plants'. The same can be said of many of the succulent genera in South Africa; the more extreme types are very local in their occurrence. But closely allied species are constantly being found; in some cases there is a series of forms between two extremes. The genus *Crassula* is full of examples of this variation which makes it difficult to delimit the species, many of which are best regarded as polymorphic. For instance, I have specimens of *Crassula perforata* Thunberg with a cartilaginous-ciliate edge to the leaves which conforms to Thunberg's original description; another plant of similar type but with slightly thicker leaves and without the characteristic edge agrees with the illustrations of Jacquin, Scopoli and de Candolle of *Crassula perfossa* Lamarck. Schonland (1929) sinks these two names into one species. In an endeavour to get more information I have consulted botanists in South Africa, several of whom have kindly sent plants of *Cr. perforata* from different localities; so far none of them agrees with '*Cr. perfossa*', but the variation they exhibit is considerable and the cartilaginous-ciliate edge is sometimes absent. The advantage of being able to study living specimens of the various forms side by side is obvious.

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GENERAL DISCUSSION

Dr. W. B. TURRILL opened the discussion by asking Mrs. Higgins whether species of *Rhipsalis* (Cactaceae) recorded in the Old World were now considered to be introductions from America. He pointed out that, in view of the well-known fact that succulents of one kind or another were found in many families not supposed to be at all closely related one to another, it was of particular importance to know how many succulents possessed the peculiar metabolism, described by Professor Bennet-Clark, and if this occurred in plants other than succulents. If it were regularly linked with succulence or occurred at all widely in succulent or other plants there was here an important physiological character showing reticulation in its occurrence with morphological characters. If a complicated series of chemical reactions could arise independently several or even many times, questions of great evolutionary importance were raised.

Sir NIGEL G. BALL, Bt.: Recent experiments carried out by Harder in Germany indicate that succulence in *Kalanchoë Blossfeldiana* depends on the length of day to which the plants are exposed. Long-day plants may develop into bushes 3 feet high with thin leaves, while plants grown under short-day conditions are only 1 to 2 inches in height, and bear a few very thick sessile leaves. Since in this case succulence is apparently due to a hormone, it is possible that in other cases also, succulence results from the presence of chemical stimulants.

Dr. A. C. HALKET: I was especially interested in the succulence of salt marsh plants referred to by Dr. Delf. As is well known, the majority of the plants which grow on the salt marshes of Britain show some degree of succulence, those, such as *Salicornia* and *Suaeda maritima* which are most frequently covered by the sea water being the most succulent.

There is evidence that the development of aqueous tissue in these plants is influenced by the amount of salt in the soil in which they grow. Plants of *Salicornia* cultivated without salt have been found to have thinner stems with a somewhat smaller percentage of water than those grown under the same conditions, except that salt was added to the soil. Also plants of *Suaeda maritima* grown without salt have less succulent leaves than those grown with salt.

Plants of *Aster Tripolium* and of *Obione portulacoides* transplanted from a salt marsh to a London garden developed thinner, less succulent leaves; while shoots of *Suaeda fruticosa* grow well in garden soil, whether heavy or light, but instead of the normal fleshy leaves produce smaller, thinner ones.

It would seem therefore that the succulence of these halophytic plants depends in part at least, on the amount of salt in the soil in which they grow.

Mr. A. H. G. ALSTON stated that he had observed that in Ceylon bulbils were never present on the leaves of *Bryophyllum pinnatum*, unless detached, while the same species when grown in England normally produced bulbils in abundance. He wished to know if the same observation applied to other species.

Professor G. D. Hale Carpenter, speaking as a zoologist interested in distribution, remarked that the speakers had mentioned America and Africa as the home of succulent plants, but nothing had been heard of Australia. He asked whether there were no succulents in Australia, and said it would seem that Australia could provide similar environmental conditions to those favouring succulents in other continents.

Mr. F. C. Grigg : A two and a half inch portion of a nine inch *Echinocactus Grusonii* that died two years before grew a well-developed callus upon the underside with root primordia while water was entirely withheld from the plant. This was rooted and is now, after a further two years, bearing four small new plants from the axils of the spines.

NOTE ON A SKULL OF HECTOR'S BEAKED WHALE MESOPLODON HECTORI (Gray) FROM THE FALKLAND ISLANDS

By F. C. Fraser,
Department of Zoology, British Museum (Natural History).

(Plates 3 & 4.)

Dr. J. E. Hamilton, Stanley, Falkland Islands, has been responsible, during his long service as Government Naturalist there, for obtaining many Cetacean and other specimens for the British Museum (Natural History). The value of the collections has been enhanced by his gifts but especially so by a skull of Hector's Beaked Whale recently received. It is of interest not only because of its almost perfect condition, but also because specimens of *Mesoplodon hectori* are very rare in any collection.

The skull with remains of dried flesh still adhering to it was picked on up the beach of one of the smaller islands of the Falkland group ; no information is available about the length or sex of the animal to which it belonged. Considering the circumstances in which it was found the specimen is remarkably complete. It had two holes in the supra-occipital region and the pterygoids were also damaged, portions of the bone in each of these places being almost paper thin.

The type of Hector's Beaked Whale was originally described as *Berardius arnuxii* by Hector (1870) but Gray (1871) realized that the differences of Hector's specimen from *B. arnuxii* were too great to allow of its inclusion in that species and established the species *B. hectori* for it. Flower (1871) included *B. hectori* in the genus *Mesoplodon* and drew attention to what he considered to be the principal difference between this cranium and that of *M. bidens* and, in fact, of all others of the genus. ' The upper extremities of the pre-maxillae are less developed laterally and less everted, and therefore approximately more of the form of *Berardius* ; but unfortunately a large piece of one of these bones is broken from the right side, or that which is usually most strongly marked, and it is impossible to say how much of the absence of the characteristic eversion may be due to the immaturity of the specimen '. The Falkland Island specimen removes any doubt about the degree of eversion of the upper extremities of the premaxillae. The skull in this region is undamaged, and the eversion is comparable to that of the other species of *Mesoplodon* and is not like *Berardius*.

Measurements of the skull for the most part compare very closely with those of the type, making allowance for the slightly greater length (14 mm.) of the former specimen, but certain of the width measurements indicate that the referred specimen is absolutely narrower than the type. Zygomatic width, basal width of the rostrum, and rostrum width at the middle of its length are all smaller in the Falkland Island specimen, but the differences are not of such a magnitude as to invalidate conclusions about specific identity.

In general, the cranium (Pl. **3**, figs. 1–3), conforms very closely in appearance to the type. The lateral basirostral groove is absent, the premaxillary foramina are level with the maxillary, and in the lower jaws the teeth are close to the apex of the mandible. As in the type (Flower, 1878), the symphysis of the lower jaw is not united, the mesorostral cartilage is entirely unossified, the elements of the occipital bone have all coalesced with each other and with the basisphenoid, the elevation of the longitudinal ridge on the upper surface of the maxilla, greater than in any other species of *Mesoplodon*, is comparable in the two specimens. The nasals are overlapped anteriorly by the premaxillae ; the right nasal and adjoining portions of the premaxillae are damaged in the type skull. The palatine is even less in evidence on the palatal surface of the Falkland Islands skull than in the other. Not only are the exposed portions narrower in the former specimen but also much shorter, the anterior tip being short of that of the pterygoid by about 5 cm. whereas in the type it reaches to within 1 cm. of the level of pterygoid anterior border. The tympanic bone length is 51 mm. as compared with 54 mm. in the type.

In the type specimen the apex of the tooth (Pl. **4**, figs. 4 & 5) in the lower jaw is, as described by Flower, exactly 1 inch (25·4 mm.) from the anterior margin of the symphysis, in the Falkland Island specimen the corresponding measurement is 11·5 mm. X-ray photographs show that the anterior edge of this tooth is approximately vertical, the posterior edge forming an angle of about 45° with the vertical. The dimensions of the teeth in the two specimens are as follows :—

	Type specimen	Falkland Is. specimen
Greatest breadth	5 mm.	4·9 mm.
Height	31 ,,	22·8 ,,
Antero-posterior length at base	28 ,,	19·3 ,,
Enamel on crown	8 ,,	7·6 ,,

As in the type the pulp cavity of the referred specimen consists of an elongated fissure, the labial and lingual portions of the root being almost in contact. This approximation is more emphasized at the middle of the aperture than at either end.

A feature not obvious in the tooth of the type specimen but present in both teeth of the Falkland skull is a very small subsidiary cusp posterior to that forming the apex of the tooth. The apex of this smaller cusp is about half a millimetre lower than the main one and the cusp on the labial side is defined by a groove extending for about a millimetre and on the lingual aspect by rather less than this.

Until the present specimen was found the species *M. hectori* was known only from the type in the British Museum and one other specimen, a skeleton in the United States National Museum, of which, according to Oliver (1922), no description has been published.

The extension of the range of this species from New Zealand waters to the Falkland Islands indicates its pelagic habit and suggests that the geographical restriction implied by the common name ' New Zealand Beaked Whale ' might be removed by referring to it as Hector's Beaked Whale.

Cranial Measurements of *Mesoplodon hectori*.

	M. hectori type Brit. Mus. mm.	Falkland Is. specimen 1949.8.19.1 mm.
Skull, total length	587, E.	601
Skull, height, vertex to inferior border of pterygoids	235	240
Skull, width at centre of orbits	228	228
Skull, width across zygomatic processes	258	242
Tip of rostrum to post. border of pterygoids, near middle line	443, E.	469
Width across occipital condyles	90	91
Rostrum, length, from level of bases of antorbital notches	343	358
Rostrum, width, between bases of antorbital notches	137	128
Rostrum, width, at middle	37	35
Premaxillae (both), width across expanded proximal ends	—	111
Premaxillae (both), width (least) opposite anterior nares	104	100
Premaxillae (both), width opposite premaxillary foramina	67	73
Anterior nares, greatest width	49	50
Maxillary foramina, least distance between	79	74
Maxillary foramina, post. border of, to end of maxillary tubercle	38	39 ca.
Vomer, as visible on palate, greatest length	89	99
Mandible, length of ramus, to end of condyle	481	498
Mandible, length of symphysis	155	161
Mandible, greatest height at coronoid process	83	91

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EXPLANATION OF THE PLATES.

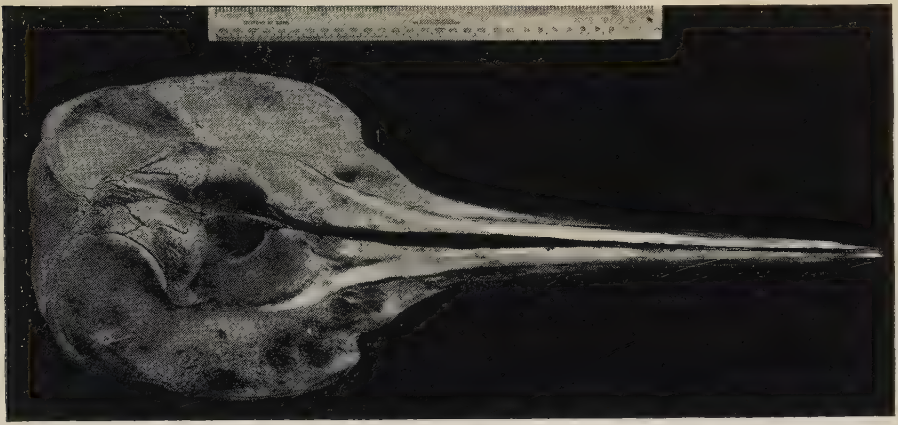
Fig. 1. *Mesoplodon hectori* skull, dorsal view.
2. *Mesoplodon hectori* skull, lateral view.
3. *Mesoplodon hectori* skull, ventral view.
4. *Mesoplodon hectori*, lower jaw, dorsal view.
5. *Mesoplodon hectori*, lower jaw, lateral view.

ABNORMALITIES IN THE SEXUAL APPARATUS OF THE COMMON DOGFISH (SCYLIORHINUS CANICULUS)

By D. R. Arthur, Department of Zoology, University of London, King's College.

(With 2 Text-figures.)

In elasmobranch fishes records of abnormalities in the reproductive system are rare. Borcea (1904) observed an unusual form of the right oviduct in *Scyllium*, and Daniell (1922) noted that in one immature *Heptanchus*, supposed



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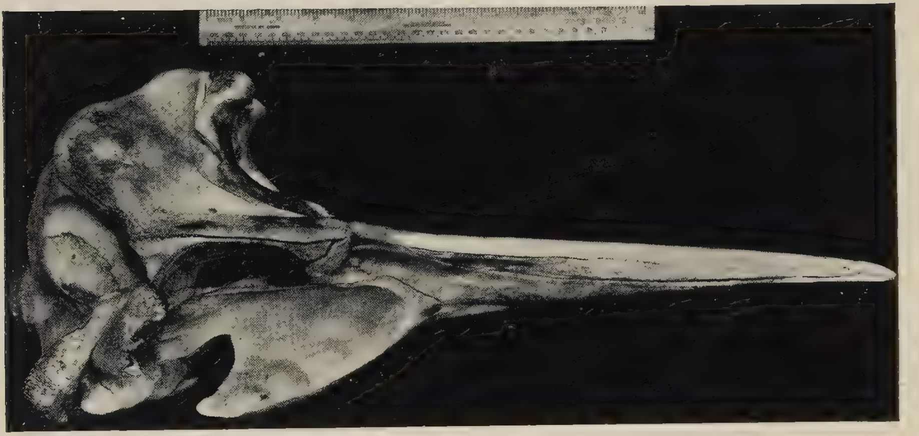

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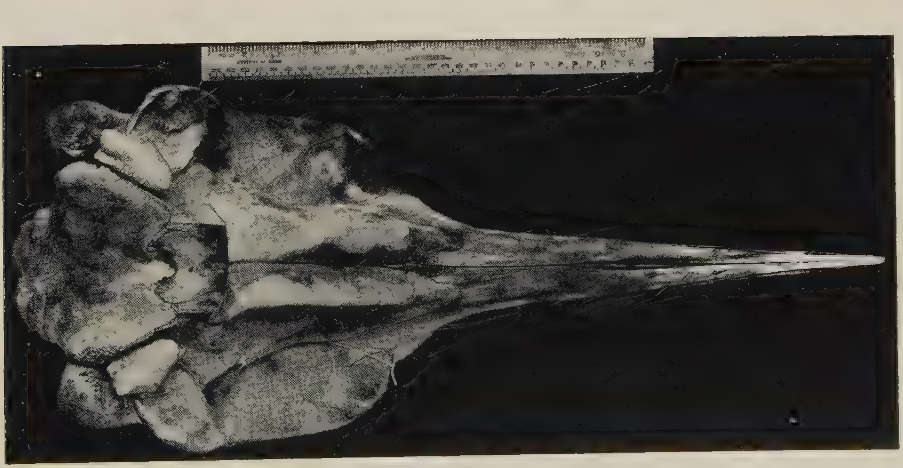

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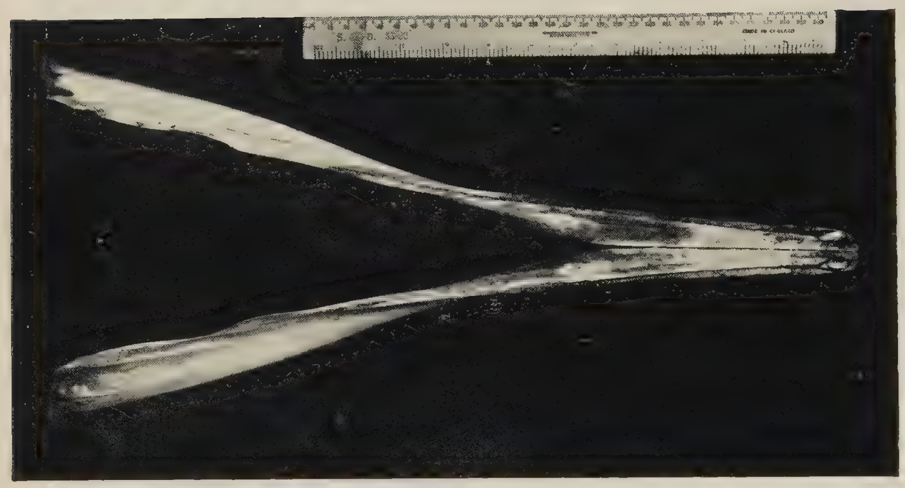
Skull of *Mesoplodon hectori*.



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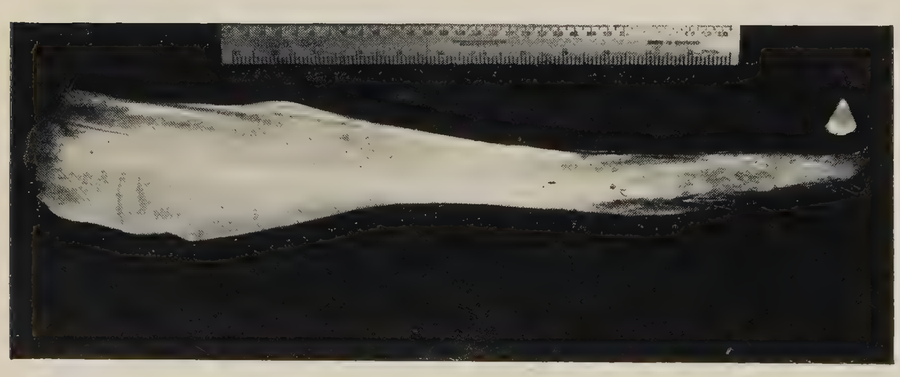

5

Jaw of *Mesoplodon hectori*.

to be a male, a rudimentary oviduct was present and one of the pelvic fins bore a clasper. In a survey of hermaphroditism in the vertebrates, Ponse (1949) gives the following records, ray (1), shark (1), lepidosiren (1) and indicates that it is a common feature in the teleosts.

During the preparation of dogfish, *Scyliorhinus caniculus*, for class-work, Mr. Charles Biddolph has observed six specimens which are abnormal in their sexual apparatus. These he has collected and preserved in formalin, and through his kindness I have been able to examine this material. All these fish came from the south Devon coast and arrived in batches of about sixty.

I should like to record my indebtedness to Professor D. L. Mackinnon for helpful criticism and advice, to Mr. Charles Biddolph for the provision of material and cutting sections, and to Mr. A. T. Green for the photographs, from which fig. 2 was traced.

Each specimen was measured from the tip of the snout to the posterior end of the first dorsal fin. In the text this is referred to as ‘length’. The pelvic fins, gonads and associated ducts were examined in detail and claspers, where present, sectioned transversely midway along their length. The gonads were sectioned at 10 μ thickness and stained with Ehrlich’s haematoxylin and eosin.

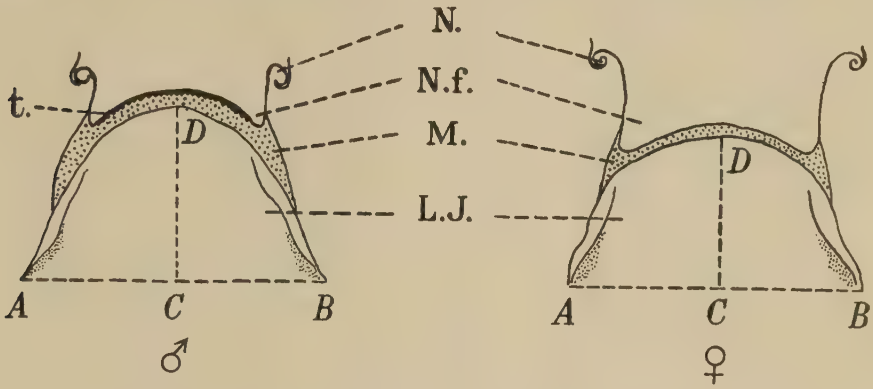

FIG. 1.—*Scyliorhinus caniculus*. External view of lower jaw of female and male. N., nostril; N.f., nasal flap; M., mouth; L.J., lower jaw; t., teeth. For further explanation see text.

Sexual differences other than the presence or absence of claspers.

Secondary sexual differences occur in *Scyliorhinus*. In the male the lower jaw curves gently to its anterior extremity while in the female the front margin is flattened (fig. 1). This is probably related to internal structure, for Brough (1937) has shown that the rami of the lower jaw in mature males are wider and more massive than those of females. The length-breadth ratio of the jaw (CD/AB) in males and females is 0·59 and 0·53 respectively.

The female teeth are small and do not extend to the margin of the jaws. In the male they are larger, have a wider distribution on the lower jaw, encroaching on its edge in the anterior region.

Observations on the sexual apparatus.

Specimen 1 (fig. 2 *a*). The fish measures 12 inches in ‘length’ and is an abnormal hermaphrodite. The teeth are large and encroach on the edge of the jaws, and between upper and lower lips is a distinct gap. The jaw structure is essentially male. The left clasper of the pelvic fin is moderately well developed and is free for the greater part of its length distally. The right clasper is indicated by a small protuberance, which is fused to the inner margin of the fin.

In normal males the inner edge of the pelvic fins are joined mesially with a slight notch posteriorly. In this specimen the fins are separate mesially, each fusing with the body wall slightly posterior to the cloacal floor. The longitudinal flap of the left clasper can be exposed by turning out the latter at right

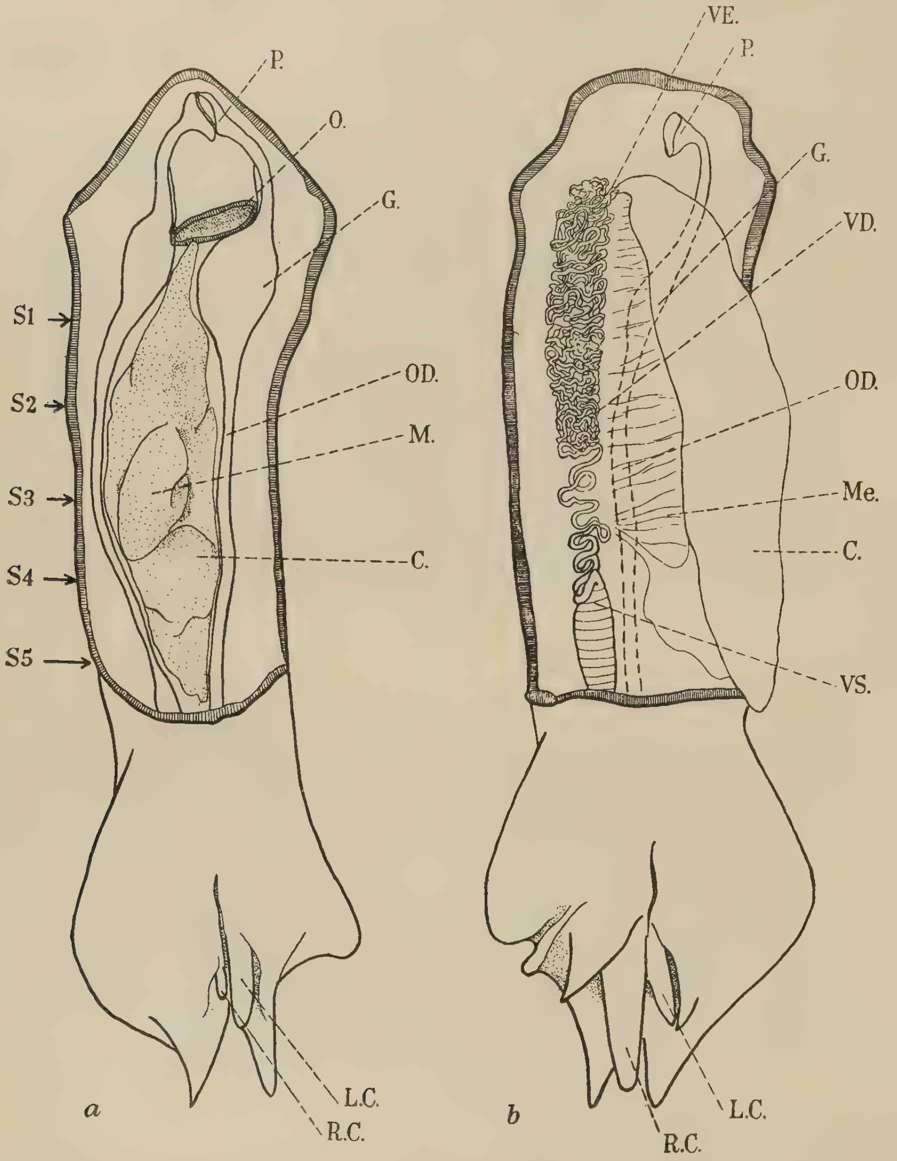

Fig. 2a.—*Scyliorhinus caniculus*. The reproductive system of an hermaphrodite dogfish (Specimen 1), showing levels at which sections were cut (S1–S5).

Fig. 2b.—*Scyliorhinus caniculus*. The reproductive system of Specimen 2, with gonad turned over to the left. The female duct of the left side is indicated by a broken line.

C., gonad; G., shell gland; L.C., left clasper; M, lobose mass attached to gonad; Me., mesentery; O., cut end of oesophagus; OD., oviduct: P., oviducal opening; R.C., right clasper; VD., vas deferens; VE., vasa efferentia; VS., vesicula seminalis.

angles to its natural position, to expose the dorsal side. This flap is absent from the corresponding right structure. Sections through the clasper do not show the normal open groove, instead the centre is occupied by a large crescentic mass of hyaline cartilage. The claspers unite the male and female during copulation, but the exact function of the siphonal-clasper complex is uncertain. It has been shown by Daniell (1922) that in *Acanthias* the sperm cells reach the groove in the claspers and are forced thence into the oviduct of the female by a current, produced by the siphon. A similar function has been suggested in *Scyliorhinus*. If this is so, then the claspers in this specimen would be non-functional.

Although the animal possesses male characters externally, the internal organs are predominantly female. The ducts are those of a mature female, with normal oviducal openings and large shell glands. The gonad is elongate and unpaired. Attached to it by mesentery, about midway along its length, is a lobose mass of tissue. Sections were cut through this and four other levels of the gonad (see S1–S5, fig. 2 *a*). Section 1, taken at the anterior end of the gonad, shows a very small portion of ovarian tissue marginally, while the remainder of the section is occupied by homogeneous, cellular material which resembles lymphoid tissue. The cells of the latter are rounded in outline, some having large irregular shaped nuclei, which almost completely occupy the cell, while others are smaller with bean-shaped nuclei.

Section 2 is midway along the elongate part of the gonad, and slightly in front of the lobose mass. It is divisible into two distinct masses histologically, connected one to the other by mesentery. The larger portion undoubtedly is mesonephric, while the smaller is composed of lymphoid-like cells.

Section 3, through the lobose mass, is made up entirely of testicular tissue. The seminiferous tubules are well developed, most having distinct lumina and showing various stages of spermatogenesis.

Section 4, taken posteriorly to the lobose mass, consists entirely of the same type of homogeneous lymphoid tissue as in sections 1 and 2. No trace of gonadial elements are evident.

Section 5, from the posterior end of the gonad, consists mainly of ovarian tissue with the eggs at various stages of development. Sparsely distributed lymphoid cells occur in the medullary region.

From these sections it appears that it is the medullary or testicular region of the gonad which has undergone change. There is a suggestion, too, of connective tissue trabeculae in the lymphoid tissue which may be the remains of the walls of the spermatic tubules. Professor Rogers Brambell (private communication 8/2/48) believes that gonads are liable to become lymphomatous and has met with something similar in X-rayed mouse ovaries.

Specimen 2 (fig. 2 *b*). The animal shows unilateral inequality of the development of the sexual organs appropriate to the sex of the animal, and the abnormal development of the ducts appropriate to the opposite sex.

The ' length ' (see p. 53) is 13 inches with very large teeth which are less evenly distributed than in normal males. They cover a wide area and extend to the margin of the jaw. Claspers are present, and are unequally developed on the right and left sides. The right is markedly stouter and longer than the left. In both, the lumen of the clasper groove is open, but no communication with the outside world via the flap is established.

The sperm sac, vesicula seminalis, vas deferens and vasa efferentia of the right side are normal. This, together with the development of the right clasper shows the right side to be typically male. On the left side an oviduct is present, but the oviducal gland is poorly defined. Dorsal to this oviduct is a male duct system. This is less well developed than on the right side ; the vasa efferentia are absent, both sperm sac and vesicula seminalis are smaller, while the vas deferens is shorter and less convoluted. On opening the sperm sacs on both sides the apertures of the ureter and vas deferens are seen, but before the latter enters the left sperm sac it is joined by the posterior portion of the oviduct. The unpaired gonad is male in character.

Specimen 3 is 12 inches in ' length ' (see p. 53) and is of interest in that it is a normal female externally, except for the presence of claspers. The teeth are small and do not encroach on the edge of the jaws. The pelvic fins are free along their mesial margins for a greater distance than in normal males. At the base are two small claspers ; they are of about equal length and only partially free distally. The gonad and ducts conform to the female pattern.

Specimens 4–6 are of interest in that they show degeneration of the gonad together with poor duct formation in relation to body size, and presumed age of the animals based on size measurements.

Specimen 4 is 15¼ inches in 'length' and is provided with two minute claspers. The oviducts are small, and it is not possible to distinguish the shell gland. The gonad is poorly developed and sections show it to be lymphoid in character.

Specimen 5 is 15½ inches in ' length '. Oviducts and ovary are poorly developed. The diameter of the oviducts is 1·5 mm., while there is no indication of the shell gland. The oviducal openings are distinct though small. Examination of the cloaca shows the hymen to be intact. The gonad is of the lymphoid type.

Specimen 6 is 14½ inches in 'length' and the width of the oviduct is only 1·75 mm. The shell gland appears as a small swelling, while here again the gonad is histologically lymphoid.

SUMMARY.

The present note describes six specimens of *Scyliorhinus caniculus* which show sexual abnormalities. Specimen 1 is an hermaphrodite fish where the gonad has presumably undergone change from the male condition. Specimens 2 and 3 show abnormal development of ducts and secondary sex characters appropriate to the opposite sex, together with unilateral inequality of the development of the sexual organs appropriate to the sex of the animal. Degeneration of the gonad and poor duct formation characterize specimens 4 to 6.

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THE HOMOLOGY OF THE MAMMALIAN PTERYGOID IN THE LIGHT OF SOME NEW EVIDENCE

By F. C. ELOFF, D.Sc.

[Communicated by Prof. G. R. DE BEER, F.R.S.]

(With 3 Text-figures.)

Since Gaupp's discovery of two pterygoid elements in *Echidna*, the compound nature of the pterygoid of monotremes and ditrematous mammals has been confirmed in a large number of forms. In the majority of cases the compound structure of this bone in ditrematous mammals is determined by the presence of the so-called pterygoid cartilage, in addition to the true mammalian pterygoid, but in a few cases a distinct second element of membranous origin was found. This has been observed by Parker in *Galeopithecus* (1885) and the pig (1874), by Broom (1914) in *Petrogale, Tatusia* and *Tamandua* and by van Kampen (quoted by de Beer, 1929) in *Erinaceus* and *Talpa.* The object of the present paper is to discuss the significance of a small membranous element found by the author in *Rhabdomys pumilio*, one of the Muridae, and which appears to be homologous with the external pterygoid plate of the alisphenoid which is present for example in man (Fawcett, 1905 *a*) and the cat (Terry, 1917).

This dermal element was found in the 23 mm. (crown–rump length) stage of *Rhabdomys*, at a stage where all the other membrane bones of the skull have already made their appearance. It takes the form of a tiny ossification, attached to the ventro-lateral margin of the ala temporalis from where it projects sideways and slightly backwards in the direction of the dentary. It appears symmetrically on both sides of the skull.

It is not the object of this article to open up the whole pterygoid controversy again. It has been fully discussed by many different authors, and is so adequately summed up by Parrington and Westoll (1940) that a further review of the whole problem is unnecessary at this stage. Only those points which have a direct bearing on this matter will be considered and attention will be focused mainly on the probable homology of the ossification in question and the morphological significance of the pterygoid cartilage.

The external pterygoid plate of the alisphenoid has always been regarded as simply an ectochondral extension of the ala temporalis, and, since similar outgrowths are known in several other cases, it would be hard to prove that it is anything else. In *Salmo* for example the epiotic develops intramembranous extensions. The dermal portion of the mammalian alisphenoid, in those forms in which it is a mixed bone, develops as an intramembranous extension of the ala temporalis and the foramen ovale of some types becomes closed from behind by a similar extension. This has been observed by the author in *Rhabdomys* and *Otomys* and possibly by Parker (1885) in *Tatusia.*

The ossification in question appears at first sight to be nothing more than an intramembranous extension of the ala temporalis but its relations to other structures point to a probable homology with a dermal bone of lower vertebrates. Its fusion with the perichondrium of the ala temporalis does not invalidate the conclusion that it represents an independent ossification since this close relationship between a membrane bone and primordial cartilage occurs quite frequently. In this same specimen of *Rhabdomys* the vomer has invaded the cartilage of the lamina transversalis posterior and the cartilage cells of the latter are continued without interruption into the osseous cells of the former. The gonial, which develops as a membrane bone just ventral to Meckel's cartilage, is firmly fused to the perichondrium of the latter in *Rhabdomys* and *Otomys* (Eloff, 1948). Although it eventually forms an integral part of the malleus, which develops out of the posterior portion of Meckel's cartilage, the gonial is the remnant of an originally separate bone and the fusion with the malleus must therefore be secondary.

It is thus quite within the bounds of possibility that the ossification under discussion is an independent element which has fused secondarily with the perichondrium of the ala temporalis. There may be some significance in the way the human external pterygoid plate, with which the ossification in *Rhabdomys* is homologized, develops. Describing a section through the head of an eleven weeks human embryo, Fawcett (1905 *a*) writes: 'The same section showed the external pterygoid plate to be membranous, i.e. not a continuation of the cartilaginous greater wing of the sphenoid'. This may signify an independent ossification of the external pterygoid plate.

In figs. 1 to 3 the relations of this ossification to other structures are shown. At first sight it does not appear to have any direct bearing on the problem under discussion, as it lies far outside the true pterygoid, but a closer inspection

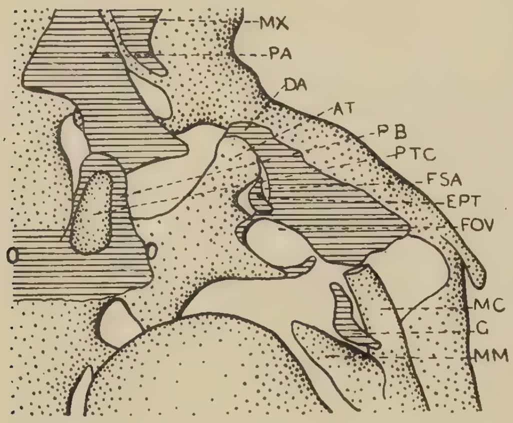

FIG. 1

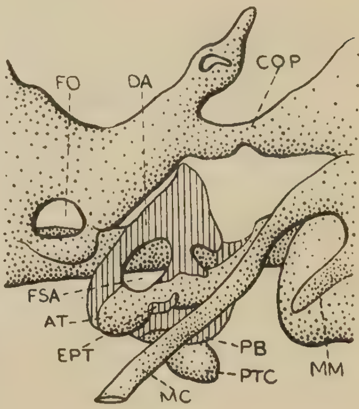

FIG. 2

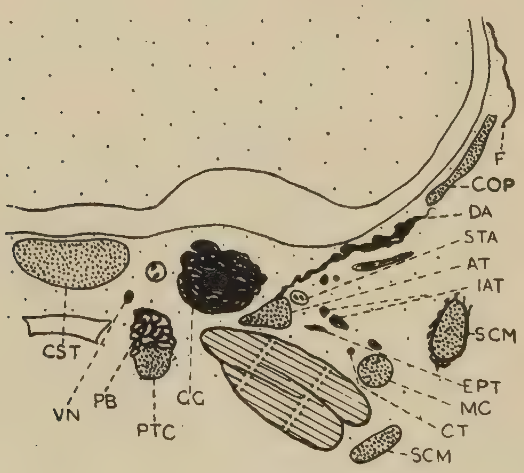

FIG. 3

FIG. 1. Ventral view of orbito-temporal region of chondrocranium of *Rhabdomys pumilio*.
FIG. 2. Lateral view of same.
FIG. 3. Transverse section through ectopterygoid region.

ABBREVIATIONS.

AT	ala temporalis
COP	commissura orbitoparietalis
CST	central stem
CT	chorda tympani
DA	dermal portion of alisphenoid
EPT	ectopterygoid (external pterygoid plate ?)
F	frontal bone
FO	foramen opticum
FOV	foramen ovale
FSA	foramen for transmission of stapedial (orbital) artery
G	gonial
GG	gasserian ganglion
IAT	inferior alveolar branch of mandibular portion of trigeminal nerve
MC	Meckel's cartilage
MM	manubrium mallei
MX	maxillary bone
PA	palatine bone
PB	pterygoid bone
PTO	pterygoid cartilage
SCM	secondary cartilage of mandible
STA	stapedial artery
VN	Vidian nerve

reveals that it probably represents the ectopterygoid of reptiles and therefore Gaupp's Echidna-pterygoid if Broom's view of the homology of the pterygoid elements is accepted. The opinion that this ossification represents the ectopterygoid was first expressed by Dr. Broom, with whom I discussed the matter. Although I found it hard to agree with him at first, after reviewing the whole question thoroughly I concluded that this was the only possible interpretation.

In my opinion it has been conclusively proved by Broom, and later by Parrington and Westoll, that the Echidna-pterygoid of monotremes is homologous with the ectopterygoid of reptiles, and I shall endeavour to prove that this membranous element of *Rhabdomys* is the homologue of these two elements.

According to Watson (1915) the Echidna-pterygoid of *Ornithorhynchus* is a large membrane bone lying ventral to the ala temporalis, with the lower surface of which its dorsal surface is in contact for some distance. In the middle of its length its upper surface just comes in contact with the lower border of the pterygoid. Further forward its inner border is nearly in contact with the palatine'.

The early contact observed between the Echidna-pterygoid and the ala temporalis in *Ornithorhynchus* seems to be a constant feature of the monotreme chondrocranium as it was found to occur in *Echidna* (Watson, 1915) as well. This peculiar relation has been retained in *Rhabdomys*, and I regard this phenomenon as strong evidence for homologizing the ectopterygoid of *Rhabdomys* with the Echidna-pterygoid of monotremes.

At first sight this may appear to be a very unusual position for the ectopterygoid, but as the palatine and alisphenoid (epipterygoid), two elements which are far apart in Gorgonopsians and Cynodonts, have moved into a position where they are in contact with each other in mammals, it is by no means strange to find the Echidna-pterygoid or ectopterygoid in close contact with the alisphenoid too, since it has always stood in close relationship with the palatine.

At this stage of development the ectopterygoid of *Rhabdomys* is far removed from the palatine and pterygoid and the relations of these three elements seem to differ considerably if *Rhabdomys* is compared with monotremes. As the palatine makes contact with the alisphenoid in the adult skull, however, a much closer relation will exist ultimately between the palatine and the ectopterygoid than is indicated by the stage under discussion, and the difference as far as these two bones are concerned will be minimized considerably.

The relations of the ectopterygoid to the true pterygoid may seem to be a serious obstacle, but a review of the history of the former will bring it into line with my contention. It has been pointed out by Parrington and Westoll that in certain Theriodonts the ectopterygoid is a bone which is apparently in process of reduction. Now, it is not difficult to imagine that with a further reduction it may have lost its contacts with the palatine and pterygoid, in the same way as it has lost its contact with the maxilla in Cynodonts and a few Gorgonopsia (Parrington and Westoll).

In other respects there is a very close agreement between the ectopterygoid of *Rhabdomys* and the Echidna-pterygoid of monotremes. In the latter group and in Theriodonts (e.g. *Cynarioides gracilis*, Broom, 1930) the Echidna-pterygoid and ectopterygoid respectively lie just on the inside of the dentary, the identical position in which the ectopterygoid occurs in *Rhabdomys*. The triangle formed by Echidna-pterygoid or ectopterygoid, Meckel's cartilage and dentary forms a very striking comparison in *Ornithorhynchus* (cf. de Beer and Fell, 1936, fig. 28) and *Rhabdomys* (fig. 3).

Further proof is supplied by the relations of the Echidna-pterygoid in *Ornithorhynchus* and the ectopterygoid in *Rhabdomys* to the mandibular branch of the trigeminal nerve. In the transverse sections given by Watson (1915), the Echidna-pterygoid lies just inside the mandibular branch of the fifth nerve which is apparently the inferior alveolar division of this ramus, as it enters the dentary bone. In *Rhabdomys* the relations are practically the same, and in fig. 3 the ectopterygoid can be seen on the inside of the inferior alveolar branch of the mandibular nerve.

A comparison of this section with fig. 28 of de Beer and Fell's paper on the development of the Monotremata (1936) shows that the relations of mammalian pterygoid, alisphenoid and Echidna-pterygoid in *Ornithorhynchus* are almost identical with that of pterygoid, ala temporalis and ectopterygoid respectively, in *Rhabdomys*. The ectopterygoid of the latter is, of course, much smaller than the Echidna-pterygoid of *Ornithorhynchus*. In both these figures the Echidna-pterygoid or ectopterygoid lies just ventral to the stapedial (orbital) artery. In *Ornithorhynchus* the artery seems to be included in a cartilaginous foramen, whereas in *Rhabdomys* it passes through a foramen whose ventral wall is cartilaginous and dorsal margin bony, being formed by the dermal extension of the ala temporalis.

Taking all this into consideration I think that there is strong justification for homologizing this membranous ossification in *Rhabdomys* with the Echidna-pterygoid of monotremes and therefore with the ectopterygoid of reptiles.

It remains to compare this element with the so-called ectopterygoids and mesopterygoids found by Broom and others in ditrematous mammals.

In his description of the development of the skull of the pig, Parker (1874) recognized three pterygoid elements which he called the external and internal pterygoid plates and a mesopterygoid. The same elements were recognized by him in Galeopithecus (1885). He regarded the internal pterygoid as the pterygoid proper, but in this he probably erred as the mesopterygoid seems to represent the true pterygoid, as has been pointed out by Parrington and Westoll. Parker's internal pterygoid in Galeopithecus and the pig seems to be homologous therefore with the ectopterygoid of *Tatusia*, *Tamandua* and *Petrogale*. The ectopterygoid of all these types, including the internal pterygoid of Galeopithecus and the pig, agree in one important respect, namely, that it stands in close relationship with the nasopharyngeal passage, which Parrington and Westoll regard as the typical mammalian condition. In *Rhabdomys* the ectopterygoid lies far outside the nasopharyngeal passage and this seems to exclude it from homology with the element which has been found in the above-mentioned types. The history of the ectopterygoid shows, however, that this is probably not its natural position, because as Parrington and Westoll point out ' there is no evidence that that the ectopterygoid habitually formed part of the side wall of the nasopharyngeal passage in normal Theriodonts '. In fact, in Gorgonopsians and Cynodonts the ectopterygoid seems to lie far outside the nasopharyngeal passage, and it is in the Ictidosaurians that the mammalian condition is approached for the first time.

The homology of the element called ectopterygoid in *Rhabdomys* with the ectopterygoid found by Broom in *Tatusia, Tamandua* and *Petrogale* and with the internal pterygoid described by Parker in the pig and in Galeopithecus is thus not entirely ruled out. The structural changes of this region of the skull are attributed by Parrington and Westoll mainly to functional changes in the jaw musculature. In rodents, with their great specialization of the jaw muscles, further changes of this region are not surprising.

If my suggestion regarding the identity of this membranous element of *Rhabdomys* is accepted, another serious problem immediately arises. In addition to an ectopterygoid, *Rhabdomys* has a typical pterygoid cartilage, which has hitherto been regarded as homologous with the reptilian ectopterygoid and monotreme Echidna-pterygoid by Parrington and Westoll or reptilian pterygoid and monotreme Echidna-pterygoid, according to de Beer's scheme of homologies. Now, with proof of the coexistence of the pterygoid cartilage, the mammalian pterygoid and the homologue of the Echidna-pterygoid both these views fall to the ground. Another explanation for the presence of the pterygoid cartilage must now be looked for.

The occurrence of secondary cartilage in connection with the development of certain membrane bones is a well-known feature of the mammalian chondrocranium. The almost universal appearance of the pterygoid cartilage among higher mammals has been pointed out by de Beer (1929). The secondary cartilage appearing in the different parts of the dentary has probably just as widespread an occurrence. In the majority of mammals there seem to be three accessory cartilages in each dentary, in others there are four, whereas in some only two are present. Accessory cartilages have also been found in the maxillary, palatine, vomer, squamosal, jugal and frontal.

In all these cases the cartilaginous nodules seem to be independent of the primordial cranium and this phenomenon has led to the almost universally accepted idea that this cartilage is of a secondary nature.

The main point, however, as far as this discussion is concerned, is that all these cartilages appear to be of essentially the same nature, differing only in some minor respects.

The first appearance of these cartilages seems to vary somewhat in relation to the membrane bones of which they eventually form a part. In the majority of cases, the accessory cartilages seem to appear considerably later than the bone. This was observed in the accessory cartilages of the maxilla and mandible of *Otomys* (Eloff, 1948), and seems to be the general rule regarding the appearance of the secondary cartilages of the lower jaw. The precursor of the pterygoid cartilage varies. In some types, e.g. *Erinaceus* (Parker, 1885), *Lepus* (Fuchs, 1910) and *Erethizon* (Struthers, 1927), the pterygoid cartilage appears first, and the bone later. In other forms this order is reversed and bone appears before cartilage, as in man (Fawcett, 1905 b), the cat (Terry, 1917) and *Otomys*. As both conditions occur in the development of the pterygoid cartilage I think one is justified in saying that there is no significant difference between the pterygoid cartilage and other accessory cartilages as far as its precursor is concerned.

The ossification of these cartilages does not seem always to follow the same course. Gaupp (1906) describes the ossification of the cartilages of the mandible as partly peri- and partly endochondral. According to Fawcett (1905 b) each half of the lower jaw of man normally ossifies from three centres, one of which is a centre for the accessory cartilages. This, however, is contradicted by Low (1905), according to whom the ossifications of the condylar and coronoid cartilaginous centra extend from the surrounding membrane bone, which led him to observe that ' these did not indicate separate elements, but were an adaptation to the growth of the lower jaw '. These observations were confirmed by him in 1910. In *Otomys* ossification of the secondary cartilages of the mandible proceeds in apparently the same way and it is probably the way in which these cartilages ossify in the majority of mammals.

Ossification of the pterygoid cartilage seems to vary. The development of the pterygoid in man, the cat and the rabbit are cited by de Beer and Fell (1936) as instances of the independent ossification of the pterygoid cartilage. In the cat Terry (1917) found evidence of two ossification centres in the internal pterygoid plate. In man the condition requires some elucidation. Although it may be deduced from some of Fawcett's descriptions that the pterygoid arises from two independent centra, in one instance (1910) he definitely mantains ' that the hamulus is ossified a little later in cartilage, but of course not by a separate centre '. From Fuch's description of the development of the pterygoid it cannot be inferred clearly whether it ossifies from one or two centra. The development of these elements are described by him as follows : 'Auf dem nächsten Stadium ist aus dem Vorknorpel typischer hyaliner Knorpel geworden. In dem mit dem Perichondrium verbundenen Blasteme treten die ersten Knochenbälkchen, unabhängig und entfernt vom Knorpel, auf.

'Der Knochen nimmt schnell an Masse zu und tritt mit der vorderen Seite und dem vordersten Teile der oberen Seite des Knorpels in unmittelbare Berührung, legt sich also hier diesem wie ein perichondraler Knochen auf. Seine kaudale Hälfte aber bleibt zunächst durchaus vom Knorpel getrennt.

'Nun umwächst der Knochen den Knorpel lateralwärts und ist dabei demselben unmittelbar aufgelagert, verhält sich also auch hierbei wie ein perichondraler Knochen.

'Hieran schliesst sich die Zerstörung des Knorpels und seine Ersetzung durch Knochen, und zwar genau nach dem Modus der endochondralen Verknöcherung. Die Zerstörung und Ersetzung des Knorpels beginnt oben und schreitet von oben nach unten fort; der Knochenersatz erfolgt im Anschluss an den dem Knorpel aufgelagerten Knochen'.

According to this the ossification of the pterygoid cartilage occurs partly peri- and partly endochondral, but as the perichondrial ossification is merely an extension of the pterygoid bone which envelops the pterygoid cartilage it cannot be regarded as a separate ossification. The endochondral centra which now appear within the eroded cartilage follow the normal course of the ossification of cartilage bone and follow probably as a matter of course upon the appearance of the perichondrial ossification. And according to Fuchs' 'der Knochenersatz erfolgt im Anschluss an den dem Knorpel aufgelagerten Knochen', which appears to denote that these intracartilaginous centra develop in continuation with the perichondrial bone.

The ossification of the pterygoid cartilage has not been fully observed in any of the types examined by the author, but in *Otomys* it follows apparently the same course as in the rabbit. In the first stage in which ossification of this cartilage was observed, it definitely seems to be the result of the encroachment of the true mammalian pterygoid, which in this case is laid down first, upon the pterygoid cartilage, after which endochondral ossification probably commences.

With regard to the ossification of the pterygoid cartilage we cannot, therefore, lay down any definite principle. Whereas it seems to ossify from an independent centre in some cases, it has been shown that in the majority of cases its ossification extends from the pterygoid bone. But even if it can be proved that the compound pterygoid of higher mammals ossifies from two separate ossification centres it will have no significance, since it has been conclusively shown that independent centres of ossification cannot serve as criteria for determining the dual nature of any bone.

The point which I endeavoured to prove in the preceding paragraphs is that the pterygoid cartilage does not differ from the other accessory cartilages in any important respect, and we have no reason for placing it in a different category. If we regard the pterygoid of higher mammals as a composite structure, bones like the maxilla and dentary have the same claim to this distinction. Why then, do we attach so much importance to the pterygoid cartilage's presence and not to the other accessory cartilages? It has been pointed out by Low (1905), Gaupp (1906), Wiedersheim (1908) and Gregory (1913) that the existence of separate accessory cartilages in the dentary does not justify the conclusion that this bone consists of different elements, and the same must hold good for the pterygoid. Even if it can be proved that this ossification in *Rhabdomys* is not the ectopterygoid I still adhere to the opinion that we have not sufficient evidence for regarding the pterygoid cartilage as a preformation of a membrane bone.

Acknowledgments.

I wish to acknowledge my indebtedness to Prof. G. R. de Beer, F.R.S., of University College, London, for his kindness in communicating this paper to the Linnean Society.

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THE OCCURRENCE OF LYSIOSQUILLA SCABRICAUDA (Lamarck) IN BERMUDA

By R. DENNELL, Zoology Dept., The University, Manchester.

Hitherto only two species of Stomatopoda, namely *Gonodactylus oerstedii* Hansen and *Pseudosquilla ciliata* (Fabr.), have been recorded from Bermuda (see Verrill, 1923). It is therefore of interest to bring to notice the occurrence there of a representative of a third genus. Through the kindness of Dr. Dugald E. S. Brown, then Director of the Bermuda Biological Station, I was able during a recent visit to examine and identify a single specimen of *Lysiosquilla scabricauda* (Lamarck) which was found swimming in Hamilton Harbour and brought living to the Biological Station. For detailed description of this species, with references, synonymy and distribution, see Miers, 1880, p. 7; Bigelow, 1894, p. 508; Kemp, 1913, p. 204; and Lunz, 1937, p. 7.

The specimen, which has been deposited in the British Museum (Natural History), is a male measuring 258 mm. from the tip of the rostrum to the posterior emargination of the telson. Miers (1880) and Lunz (1937) state that the dactylus of the raptorial claw bears 9 or 10 strong teeth, and the Bermuda specimen bears on each dactylus 9 well-developed teeth, including the spinous tip of the dactylus itself, but proximally there is a minute incipient tenth tooth. Each propodus bears 4 movable spines proximally. The colour of the body in life was precisely as described by Lunz (1937).

Whether the fact that this specimen was taken while actively swimming indicates that, like *Chloridella empusa* (Say) (see Brooks, 1886, under *Squilla* *empusa*, p. 51), *Lysiosquilla scabricauda* moves considerable distances from its burrow, or whether it was dislodged by the heavy seas caused by the hurricane of two days previously (13 September 1948), is not clear.

Gonodactylus oerstedii is found from Brazil to the West Indies (see Kemp, 1913, p. 204), and *Pseudosquilla ciliata* has a wide distribution in Indo-Pacific and Atlantic waters (see Kemp, 1913, p. 100). As previously stated, both occur in Bermuda, and since the Stomatopoda inhabit only relatively shallow waters and these islands are separated from other land by 700 miles of deep ocean, their distribution in the Western North Atlantic must be partly accounted for by the extensive drift of their slowly developing larvae in the clockwise current of the Gulf Stream. It may be noted that the larva of *Pseudosquilla ciliata* has been recorded from the Sargasso Sea (see Kemp, 1913, p. 100). The discovery in Bermuda of *Lysiosquilla scabricauda*, already known from the West Indies (Lunz, 1937, p. 8) is therefore not surprising, and it may be expected that other Stomatopoda may be found there.

I am indebted to Dr. I. Gordon for advice and help with the literature.

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PROCEEDINGS OF THE GENERAL MEETING ON 23 February 1950

Professor F. E. FRITSCH, F.R.S., President,
in the Chair.

The Proceedings of the General Meeting held on Thursday, 9 February 1950, having been circulated, were taken as read and confirmed.

The following were thanked for gifts made to the Library since the last Meeting :—Dr. E. C. Barnett, Mr. J. M. Black, Flt.-Lt. A. J. Cork, D.F.M., Professor F. J. Lewis, Dr. Ernesto Marcus, Mr. E. A. Robins, the Royal University, Uppsala and the Fisheries Department, Hong Kong.

The following Fellow signed the Obligation in the Roll and Charter Book and was admitted a Fellow :—Miss Elisabeth Anna Ullmann, B.Sc.

A DISCUSSION ON MORPHOLOGY AND FINE STRUCTURE was opened by Dr. C. F. A. PANTIN, F.R.S., Dr. J. R. BAKER, Dr. L. E. R. PICKEN and Mr. J. R. G. BRADFIELD.

In the general discussion the following took part :—Dr. G. Bourne, Dr. Helen Brown and Dr. M. Pryor ; Dr. Pantin replied.

DISCUSSION ON MORPHOLOGY AND FINE STRUCTURE

INTRODUCTION

By C. F. A. Pantin.

Before listening to the principal contributors to the discussion I should like to consider why this question is important and particularly why it should be so for our Society.

All biologists are interested in the nature of vital structure, and in the last decade certain new principles have emerged in relation to it. One hundred and fifty years ago biologists well knew that the relationships of organisms showed a significant plan. There was not just a random assemblage of every kind the mind can conceive. The evident species, classes and types made it apparent that there was a natural classification independent of the observer. While a few, like Lamarck, gave an evolutionary explanation of this plan, the majority explained the phenomena in quite a different way. The classificatory plan, the unique character of species, adaptation and homology were deemed to be part of an underlying ideal plan of nature. In much the same way, to-day we can look upon the classification and relation of the elements in the periodic table as evidence of such a plan. Such a plan was frequently considered as the expression of a Divine Idea. In 1802 Paley (1849) inferred the existence of design in nature by considering adaptation. Louis Agassiz (1859) in his *Essay on Classification* attributed a divine origin to the classificatory plan in the very year of publication of the *Origin of Species*.

But whether or not the plan was divine, the notion that the structure and relations of living organisms were pre-determined by an ideal plan of any kind seemed to be swept away by Darwin's work. Classification and homology received an evolutionary explanation, whilst adaptation became the negative image of natural selection.

But the idea of an underlying plan survived implicitly in an unexpected place ; in our schools of physiology. Often to the exasperation of the zoologist, the physiologist in the past has not infrequently treated the ' lower ' animals as so many stages between amoeba and man ; an idea not altogether removed from the old *scala naturae* of the 18th century and earlier, and not diminished in force by a training based on selected types. Information about the complex structure, as well as about the function of ' nerve ', was to be gained equally from the study of the nerve cells of Crustacea as from the sciatic nerve of a frog. Yet the resemblance between such structures is certainly very different from one based on evolutionary homology. Some of the most interesting work at the present time on the relation of the behaviour of animals to the structural machinery by which it is executed is that of Professor J. Z. Young (1950) on the relation of the process of learning in Cephalopods to the structure of their central nervous system. Not the least remarkable feature of this work is that it should have any relevance whatever to the relation between learning and brain structure in ourselves. Evolutionarily the brains of Cephalopods and Vertebrates are utterly sundered. How does it come about that not once but many times a highly complex mechanism to meet the requirements of behaviour has been built up on principles so similar that valid information about the one can be obtained by study of the other ? The problem here is essentially the same as that which exercised Bergson (1911) when he drew attention to the astonishing similarity between the eye of a Cephalopod and of a Vertebrate ; though I see no reason to accept the conclusions he drew from the comparison.

Though the idea of an ideal plan has—curiously enough—long been implicit in the mechanistic outlook, it is only recently that it has emerged explicitly. Perhaps the first realization of this followed the discovery by Fletcher and Hopkins (1917) of the significance of carbohydrate metabolism in vertebrate muscular contraction. Though our views of muscular metabolism have changed enormously since then, their work brought to light a metabolic process which proved widespread among living creatures and which showed some relationship even to such different activities as the alcoholic fermentation of yeast. It soon became apparent that at the chemical level there was a whole series of biochemical parallels between the metabolic processes of widely separated organisms ; parallels which certainly had no simple evolutionary origin comparable to that to be inferred from homologous structures.

These biochemical parallels have their origin in the limitations imposed on vital systems by the unique properties of matter and energy as we find them in the Universe (Pantin, 1932). The old evolutionary interpretation treated form as though it were moulded, like putty, from statistically numerous small random variations. But this interpretation is only in part correct. The materials from which organisms are built up are not so much comparable to putty as to the standard parts of a child's constructional set : each part with its limited qualities of structure and of potential function (Pantin, 1950). In combination these standard parts can build certain kinds of structures of a higher order with emergent properties, and the number of these kinds is limited.

The emergent properties of the standard material parts out of which organisms are necessarily constructed are now being found to be of increasing significance in determining structure. And these emergent properties result in structural parallelisms between evolutionarily separated organisms of quite a different kind from those ordinarily considered in the concept of evolutionary homology.

It may be contended that while all this may be of interest to the biochemist it has little to do with the zoologist interested in the variety of animals and their systematic relations. Such a contention would be very wrong, as an illustration will show. In the classification of the Coelenterata, the major groups are divided by features of evolutionary significance comparable to characters, such as those of the teeth or limbs, upon which the Vertebrates are classified. In the Coelenterates, we have for instance the varied patterns of the mesenteric cycles of the Actinozoa which divide the Actiniaria, the Ceriantharia, the Zoanthinaria and so on. But perhaps the most important recent work relating to the systematics of the Coelenterates is that of Weill (1934) on the comparative morphology of cnidae. Yet in this case similar morphological complexity in two nematocysts may mean something quite different from the similar morphological complexity of two pentadactyl limbs. Such structures are produced by the orderly secretion of protein molecules. Similarity of complex form in these cases may be comparable to the intricate similarity of two snow crystals ; a similarity which can scarcely be said to be of evolutionary origin. We are dealing with a morphology with new and unfamiliar rules.

Structural resemblance determined by the unique properties of matter are to be seen at all levels of structure, but they are peculiarly evident in the smallest structures. The remarkable morphological convergences to be seen in evolutionarily distinct stocks of flagellates and algae have been strikingly demonstrated by our President in the opening chapters of his great work on the Algae (Fritsch, 1935).

For these reasons a study of fine structure and of the peculiar laws which govern chemical morphology are of the utmost interest to physiologist and systematist alike.

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STUDIES NEAR THE LIMIT OF VISION WITH THE LIGHT MICROSCOPE, WITH SPECIAL REFERENCE TO THE SO-CALLED GOLGI-BODIES

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It must be explained at the outset that what I have to say lies only on the fringe of ' fine structure ', since I am interested in objects that are just large enough to be studied effectively with the light-microscope.

Histological staining was tried by Leeuwenhoek in 1714, but the method was only used sporadically up to the decade beginning in 1848, when it was rediscovered by several microscopists and soon began to find general favour (Baker, 1945). It became apparent that cells would only stain in the desired way when they were dead, and a multitude of methods of fixation was tried, until the use of the well-known routine fixative mixtures became established.

Morphological studies received an enormous impetus from two quite distinct sources at about the same time. One was the rediscovery of staining, which made micro-anatomy very much easier ; the other was the publication of the *Origin of Species*, which made it very much more interesting, because biologists now had the fascinating new task of establishing phylogenetic relationships by studies in comparative anatomy and embryology.

Researches of this kind jumped forward when paraffin embedding and serial microtomy were introduced. One fixed the tissues, embedded them, cut serial sections, and applied stains : micro-anatomy was rendered immensely easier than it had ever been before. There was complete agreement between the knowledge obtained by this new method on the one hand and that obtained by fine dissection on the other, so far as the latter could carry the investigator, and the new method was therefore regarded as reliable when it went beyond the limits of control by dissection : indeed, the reliability of the whole technique of microtomy seemed so obvious that it was scarcely questioned.

Meanwhile a new kind of study was being undertaken, which would strengthen even further the general belief in the validity of the routine methods of research in micro-anatomy and histology. This was the study of chromosomes. It was found that these were the easiest things in the cell to stain deeply, and the regularity of their behaviour soon attracted attention. When, just after the turn of the century, Sutton (1902) pointed out the exact correspondence between the distribution of chromosomes on the one hand and of genes on the other, attention became focused even more firmly on these particular cellular constituents. As the subject of chromosome-cytology and of genetics became rapidly more exact and at the same time more elaborate, the correspondence that Sutton had pointed out became more and more evident.

Although nowadays smears and squashes are much used, yet nearly all the work that founded the hybrid subject of cytogenetics and proved the chromosome theory of inheritance was done on stained sections. Since the behaviour of the chromosomes exactly corresponded to the behaviour of the genes, as determined by experiments in hybridization, it was clear that students of the chromosomes must be seeing them as they really were : in fact, it scarcely ever entered any one's head to doubt this. Just occasionally some one looked at a living chromosome and noticed that it resembled what was seen in a preparation that had gone through the ordinary routine (Bělař, 1929) ; but not much notice was taken of this, for scarcely anyone doubted the general validity of the standard methods of microtomy.

Comparative anatomy and embryology on the one hand, then, and cytogenetics on the other, caused biologists to believe in the genuiness of the appearance of tissues and cells as seen in ordinary microscopical preparations. One slight doubt was occasioned by the mitochondria : it was known that they could be seen in the living cell, but that certain particular fixatives must be used if they were to be seen in sectioned material. They were to some extent studied in the living cell, but for the most part they continued to be examined in sections, and the mitochondria of most kinds of cells are only known from observations of the latter kind.

I do not believe that the degree of shrinkage of cells caused by the routine processes of fixation and embedding are generally realized. I wish I could persuade people to measure cells when still alive in the body-fluid of the animal or in a suitable saline solution, and then to measure the same kind of cell in a microscopical section. Quite usually the linear measurement has been reduced to one-half, so that the volume has been reduced to one-eighth of what it was. If a protein precipitant was included in the fixative, large holes will also have been torn in the ground cytoplasm and nuclear sap, which were optically homogeneous during life. These holes tend to be overlooked, but they can easily be seen by cutting extremely thin sections and staining deeply. Cellular morphology cannot be properly investigated under these conditions.

Two objects suffer most—the so-called ‘ resting ’ nucleus and the Golgi bodies. It is a strange fact that we cannot interpret the picture of the resting nucleus as seen in a routine microscopical slide. What are the lumps that stain with basic dyes ? Are they the heterochromatic segments of the chromosomes ? Or do some of them represent desoxypentose nucleic acid that was dispersed in the nucleus during life and has now been coarsely precipitated ? Does desoxypentose nucleic acid ever exist except in relation to the chromosomes ? We do not know the answers to these important questions.

I shall devote the rest of my time to the Golgi bodies.

There are three principal ways in which a transparent and colourless cellular constituent may be rendered evident in the field of view of the ordinary microscope : a coloured substance that is not a dye (e.g., sudan black) may be dissolved in it ; or it may be dyed ; or it may be impregnated with a metal. The latter method was introduced by Krause in 1844. Certain tissue-constituents readily reduce silver nitrate or osmium tetroxide and thus cause the formation of a black or blackish precipitate. The method was used at first mainly to indicate cell-boundaries, but by the seventies it had come into general use for darkening the axons of nerve-fibres and thus making it easy to trace their courses (see, e.g., Frey, 1871). In 1880 Golgi was fixing nervous tissues in a mixture of potassium dichromate and osmium tetroxide and subsequently impregnating with silver nitrate. Eighteen years later, having used a method of this sort on the cerebellum of a barn-owl, he noticed in the cytoplasm of the Purkinje-cells the black network to which his name has ever since been attached (Golgi, 1898).

By this time the belief in the validity of the routine methods of microtomy had become so firmly established that it occurred to no one to question them. One might have supposed that cytologists would have set themselves to discover whether a network resembling Golgi's occurred in the living cell, but this was not so ; they set themselves quite a different task, namely, to find the surest methods of exhibiting Golgi's net. It is quite clear from the literature that this was the intention. If spheres were seen instead of a network, the procedure was changed until the net was produced. Thus Addison (1937) wrote, ' When the coloration [of the Golgi element by silver] is intense but somewhat granular one may try adding to the fixative ethyl or methyl-alcohol. . . . With this formula successful preparations show the Golgi net dark grey on a bright yellow background '. Success meant a net.

There is nothing in the whole of the rest of science that can be compared to the investigations undertaken in this spirit. It is with the greatest difficulty that one can understand how work of this kind survived so long. The only possible explanation is the enormous prestige of the microtome and of the routine associated with it, which had brought people to the belief that one really could not investigate the morphology of the cell while it was still alive.

The first person to investigate on a large scale the validity of the routine Golgi methods was the French cytologist Parat, who directed his microscope towards that part of the living cell in which these methods showed a network (Parat, 1928). He saw there no net : on the contrary, he saw separate spheres, and these he called neutral red vacuoles, because he was accustomed to colour them in the living cell with neutral red. If what Parat said were true, the Golgi workers had been studying an artifact. Their reaction was immediate and violent : abuse took the place of argument and Parat's work was almost swamped under the weight of it. An early death by shipwreck removed one of the best cytologists of our time.

The policy of our group of cytologists at Oxford—Dr. O. L. Thomas (1947, 1948), Dr. A. J. Cain (1948), Dr. H.-S. Wu and myself, with help from Miss B. M. Jordan and others—has been to follow in Parat's footsteps by basing our conclusions on what can be seen in the living cell. Our work has fallen into three parts.

First, we have tried to discover accurately the morphology of the bodies in the Golgi zone. In this we have relied largely upon the simple but effective form of phase-contrast microscope devised by Dr. O. L. Thomas, Mr. D. A. Kempson, Mr. P. C. J. Brunet and myself (Kempson and others, 1948 ; Baker and others, 1949). We agree with Parat in denying the existence of any Golgi network in the living cell. We find instead separate spherical or spheroid bodies. We differ from Parat in stressing their lipoid nature. Some of them, especially the small ones, appear to be lipoid all through ; others to contain a spherical vacuole or vacuoles of non-lipoid material within, so that the lipoid is in the form of an enveloping sheath or externum.

Secondly, we have sought to invent methods of preserving the true form of the Golgi bodies in fixed preparations. We have worked with cells that can be easily examined during life, so as to know for certain whether the techniques used do in fact maintain the bodies in approximately the living form. When that is achieved, the techniques may be applied with some confidence to other cells that cannot easily be exposed to study during life. The sudan black technique (Baker, 1948) is a considerable step in this direction, and I am at present trying to improve it. It is important to stress the radical difference between our procedure and that of those who have devised the standard Golgi techniques. We are trying to render permanent what can be seen in the living cell.

Thirdly, we have tried to find the chemical composition of the lipoid of the Golgi bodies. Some time ago I carefully reviewed the literature of this subject, and concluded that no reliable information was available (Baker, 1944). I brought forward strong evidence of my own, not amounting to rigorous histochemical proof, that an important constituent was phospholipine, as had often been suggested. It appeared necessary to devise a reliable test for this group of substances, and this was done (Baker, 1946 and 1947). Using this new method, Dr. Cain was the first to provide valid histochemical evidence of the existence of phospholipine in the Golgi lipoid (Cain, 1947). A positive reaction is, however, by no means always given, and it seems probable that other lipoids are present in addition, which may mask the presence of phospholipine. It is now a matter of great interest to identify the other lipoid or lipoids. It will not surprise me if it be found that triglyceride is present.

The view of the nature of the Golgi bodies that has just been presented is powerfully supported by two papers of particular interest recently published by Palade and Claude (1949 *a* and *b*). The actual constituents that represent in life the network of the standard Golgi preparation are, according to them, spheres containing phospholipine. They have made a very detailed study of the origin of myelin forms from these spheres as a result of the action of the routine Golgi reagents. It is these myelin forms, blackened by the reduction of silver nitrate or osmium tetroxide, that constitute the Golgi net. The work of Palade and Claude will clear away much of the mystery that has surrounded the Golgi bodies and help to place the whole subject on a more scientific basis. Although their views accord in some respect so closely with my own, it is necessary to enumerate four points in which I find myself in disagreement with them.

First, I think they are mistaken in supposing that the spheres or spheroids are always lipoid all through. On the contrary, it seems to me from studies of the living cell that they often consist of a lipoid externum and a non-lipoid vacuole.

Secondly, I deny that the Golgi bodies of germ-cells are of a different category from those of somatic cells. I do not understand how anyone who has examined both kinds of cells could maintain the view that they are essentially different. The Golgi bodies of the female germ-cells have been traced through into those of the embryo. It must be allowed that in a few cases (especially the primary spermatocyte of the snail) the aspect of the Golgi bodies is strange, but this is not true of germ-cells as a whole.

Thirdly—and this is particularly important—Palade and Claude do not allow a connexion between the lipoid spheroids and the process of cellular secretion. This connexion, long ago described in the case of the secretion of the acrosome of the spermatozoon and clearly recognized in somatic cells by Nassonov in 1923, has been established by the labours of many cytologists, particularly Hirsch (1939). The evidence is massive and cannot simply be disregarded. Innumerable cases of the participation of the Golgi bodies in cellular secretion have been described; indeed, one might almost say that the difficulty is to quote cases in which they are known not to participate, except in the production of carbohydrate and cuticular secretions. Worley and Worley (1943) have actually watched them performing the processes of cellular secretion in the living cell. The usual process seems to be as follows:—a lipoid spheroid develops a vacuole or vacuoles within it; the secretion-product accumulates within the vacuole; and the lipoid externum is eventually cast off.

Lastly, I do not understand the outlook of Palade and Claude on their own work. Their attitude would appear to be this: the Golgi net is an artifact; the reality is merely spheres containing phospholipine; therefore there is no Golgi element and nothing of interest to study. On the contrary, the existence of these spheres in nearly every animal cell, usually in a particular place in it, is of high general interest. The fact that one now knows the real form of these bodies, instead of seeing a distorted artifact, by no means reduces their intrinsic interest: quite the contrary.

It is not because I undervalue the work of Palade and Claude that I enumerate these objections. I appreciate its value highly, but consider that they have not placed their own valuable contribution in the right perspective in the Golgi controversy.

Since the particular artifact studied by Golgi represents so badly what is actually present in the living cytoplasm, it no longer seems desirable to connect the great neurologist's name with this cellular constituent. A descriptive name is surely preferable. Ries's name 'Lipochondrien' (Ries, 1935) is convenient, but a Greek ending is more suitable for a word that must be used internationally. I therefore suggest *lipochondrion* (plural *lipochondria*). The following definition may serve :—

> Lipochondria are spherical or subspherical lipoid particles of different sizes contained in the cytoplasm of a cell. They are visible during life and often have a particular affinity for neutral red in the living cell. The lipoid reduces osmium tetroxide much more slowly than do globules consisting wholly of fat (triglyceride). Lipochondria are not preserved by the ordinary histological routines (for instance, Bouin's or Zenker's fluid followed by paraffin embedding). In many kinds of cells the lipochondria are confined to a particular place in the cytoplasm, usually near the nucleus ; the place is characteristic of the particular kind of cell concerned and the centre of it usually lies in the main axis of symmetry of the cell, if the cell has such an axis.

The name *lipochondria* (=lipoid granules) provides a convenient contrast with *mitochondria* (=thread-granules). Mitochondria differ markedly from lipochondria in their strong tendency to appear as rods or threads, in their uniform diameter in the great majority of cases in any one cell, and in their relatively low lipoid content (caused by the large amount of ribonucleoprotein in them).

Lipochondria have been known for well over a century. They were figured and described by Valentin in 1836 in the nerve-cells of various vertebrates (see especially his figs. 45 and 49 on Tab. VII). He describes them in fishes (p. 138) as being 'small, dispersed, separate, round particles'. In the celebrated *Mikroskopische Untersuchungen* (1839, p. 182), Schwann also mentions that the contents of ganglion-cells are finely granular, and it therefore seems probable that he saw the lipochondria.

The main ideas I hope to leave with you are these. The routine methods of microtomy have resulted in great advances in the fields of micro-anatomy, comparative embryology, and chromosome-cytology ; but they tend to lead us astray when the objects we want to study are very small and have little resistance to the ordinary reagents used in microtomy. It is altogether a mistake to suppose that an investigation of the structure of the living cytoplasm is impossible. The subject has been so much neglected that one has only to look carefully to make important discoveries.

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FINE STRUCTURE AND THE SHAPE OF CELLS AND CELL-COMPONENTS

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The summaries submitted by contributors to this discussion showed that the term ‘ fine structure ’ was interpreted in different senses by different speakers, and it is perhaps worth calling to mind the history of the term. It was first used in a special sense as a translation from the German of Richard Herzog (1932), who had used it to mean ‘ molecular texture ’ : ‘ The application of X-rays to the study of natural fibres and membranes has made it possible to establish a link between fine structure and chemical structure, as in the case of true crystals ’. In this sense it was used in the title of a review : ‘ The Fine Structure of Biological Systems ’ (Picken, 1940), and it still provides a convenient designation for the realm of organization between individual molecules on the one hand and microscopic structures on the other. F. O. Schmitt (1939 *a*, *b*) had coined the term ‘ ultrastructure ’, but it seemed preferable to use normal English in an enhanced sense, and to translate the earlier German term *Feinstruktur* as ' fine structure ' ; more recently Frey-Wyssling (1948) called his book *The Submicroscopic Morphology of Protoplasm and its Derivatives*, but the term ' fine structure ' occurs over twenty times in the indexes. The usefulness of the term seems to outweigh certain disadvantages ; for example, ' fine ' has several meanings in common speech which might mislead the general reader, and the term ' fine structure ' has long been used by spectroscopists with reference to the detailed structure of spectral lines. It may be argued that there is a real advantage to biologists in reserving the term for molecular texture beyond the limit of resolution of the light microscope.

Looking back over the years it seems that a most important change in our outlook on the nature of living matter—perhaps the most important change since the cell-theory itself—was taking place about fifteen years ago. It was the gradual recognition that one by one various structures in the cell, as well as structures formed outside cells or by aggregates of cells, had been shown to be not amorphous, but in greater or lesser degree, oriented. By amorphous is meant, having their component molecules arranged in space entirely at random, as in the classical conception of a liquid or glass. Though, as Sir D'Arcy Wentworth Thompson showed, Nature may act in some senses as a potter or glass-blower (Thompson, 1917), it became clear, some ten years ago, that she does not do so in the sense that her materials are amorphous. All biological structures appear to possess to some extent an oriented texture.

So long as biological structures were regarded as amorphous, they were separated by definition from the inanimate world of crystals ; and their assumption of specific shapes, and their growth, were phenomena without point of contact with the non-living world. This statement does not ignore the many demonstrations of quasi-natural shapes assumed by liquid drops, or by systems in which surface tension plays a formative role. But it was always clear, that these systems provide but remote analogies to the phenomena they simulate ; in composition they are for the most part utterly unlike living systems ; whereas many of the natural fibres of proteins and cellulose (on which depends our knowledge of fine structure, and of the physical properties associated with certain types of molecular texture) are the result of the growth and transformation of living cells.

When it was shown that the various types of biological structures possess an ordered molecular texture, it became clear that the forces which act in bringing them into being, in causing their substance to increase, or in causing them to multiply, may be related to the forces responsible for the appearance of order from disorder in inanimate systems. Though cells do not increase by a process analogous to crystallization, their parts (it now seems) may well do so.

' Growth ' (it has been written) ' does not result from a force resident in the whole organism ; rather does each individual elementary particle possess an independent force —an independent life, we may say ; that is, the molecules are so assembled in each elementary particle, that they exert a force by whose action each is enabled to attract new molecules and so to grow. . . ' This passage is translated from Schwann, co-creator of the Cell-Theory, writing in 1839. Writing in 1946, ten years after the change in outlook already referred to, Hinshelwood ventures to say : ' The synthesis of a protein partakes of the nature . . . of crystal growth '.

It is desired to stress the clue given by the observed ordered molecular texture of living structures to the forces at work in their genesis and maintenance, because it seems, in certain instances at least, that the transformations in shape which many cells undergo in the course of ontogeny are intimately associated with the oriented increase of parts of the cell.

My attention was first drawn to changes in shape in relation to changes in fine structure by the work of Pattri (1932) on the onset of birefringence in the modelling of the head of the sperm of *Liogryllus*. Pattri showed that birefringence first appears when the head, which starts by being somewhat turnip-shaped, begins to elongate. The longer and narrower the sperm-head becomes, the greater its birefringence. Many of the extraordinary spermatozoa of arthropods invite examination in the light of this work ; for example, the sperm of a millipede, *Glomeris marginata*, described by Bessière (1943) as an elliptical lemon-squeezer. There are many other instances where cytological observations suggest that a change in texture, resulting in the increased orientation of chromatic or other portions of the cell, may lead to deformation and the assumption of a characteristic shape.

My own work on the relationship between shape and fine structure in the scales and bristles of insects started from the realization that in many instances where the fine structure of elongated cells has been examined (for reasons not at first sight related to the interests of the biologist) it has been found that long chain-like molecules, or molecular aggregates, are oriented in the surface membrane, or in the substance of the cell, so that the direction of the molecular chains is related to the long axis of the cell. In the keratinized cells of the hair cortex, as well as in the axons of nerve-cells or in muscle-cells, for example, the long axis of the cell runs parallel to the direction in which long-chain molecules are oriented in the substance of the cell. In other instances—in the cellulose fibres of certain plants, for example—the oriented chain-molecules lie in the surface of the cell, in a surface membrane. Sometimes the molecular axis is parallel to the cell-axis ; at others it may be transverse, or inclined to that of the cell at a constant or varying angle. These several types of elongated cell are produced by the transformation, in the course of differentiation, of more or less spherical cells. At the time when this work was undertaken, what happens in the course of differentiation was not known in a single instance. It was not known at what point in the history of the cell orientation of its substance occurs, or to what extent the onset of orientation is correlated in time with the change in shape. It was conceivable that cells first elongate and subsequently develop orientation ; and in order to examine this point in one case, a study of the development of the scales of Lepidoptera was begun.

The scales are tubular outgrowths from more or less spherical cells and are filled with cytoplasm. The outgrowths elongate progressively and are gradually transformed into a great variety of structures. A particular study was made of the developing scales on the wings of the Meal Moth, *Ephestia sericarium* (Scott). In order to detect changes in orientation, the material was examined under the polarizing microscope at successive stages in its development ; and it was possible to obtain confirmatory evidence of orientation, in certain types of mature scales, by taking X-ray photographs. It was found that, from the time of their emergence as tubular outgrowths about 6 μ long, the scale-rudiments are birefringent (Picken, 1949). Although the scales on the lateral margins and on the body of the wing become flattened, they are largely composed of oriented material even at the end of their development, as shown by their birefringence and by X-ray photographs. The X-ray diagrams are recognizable as variants of that of chitin.

In one type of elongating cell, therefore, there seems to be some correlation in time between the onset of change in shape and a change in orientation. In the scales of Lepidoptera, as for that matter in the bristles of *Drosophila* (Lees and Picken, 1945) orientation (revealed by birefringence) is present as soon as the elongating rudiment can be recognized. The scale or bristle rudiment does not grow as a tube of amorphous material on which orientation is secondarily imposed ; it consists from the beginning, in part at least, of oriented material. The systematic distortions which are to be observed as the scale assumes its definitive shape modify, but do not destroy, the fibrillar organization of the rudiment. Indeed, even in the most extravagantly shaped scales, the contours of the scale reflect the distribution of the oriented material.

It is suggested, then, that in a number of different types of cells, changes in shape are associated with changes in fine structure, and more precisely with changes in orientation. These changes may occur in the substance bounding the cell-contents or in the cell-contents themselves. In some instances there may be a causal relation between changes in orientation and changes in shape, such that changes in shape are the result of changes in orientation. That is to say, cells may be deformed, as it were, by the growth of fibrils in their substance. But it seems probable that the growth of an insect scale or bristle, or the elongation of a phloem cell or root hair in a plant, are phenomena of a higher order of complexity. We cannot explain the origin of orientation by any simple mechanical hypothesis ; and to say that shape and orientation are correlated does not imply any simple mechanical explanation of cell-elongation.

The functional significance of changes in fine structure has been ignored in this brief statement, but it must not be forgotten that the phenomenon of muscular contraction has its morphological aspect, and the transformation of a contracted muscle fibre to an extended fibre may be analogous to the conversion of some types of short fat cells into long thin cells as a result of a change in molecular texture. Nature provides working models of this change in many ciliates, for example the Swan Animalcule, *Lacrymaria olor*, which in the twinkling of an eye changes from the shape to which its name is due to something resembling a stoppered phial, as a result of the contraction of its myonemes, that is, as the result of a change in texture of protein fibrils lying under the pellicle. In contrast to examples mentioned earlier, these are changes in shape at approximately constant volume and in the absence of growth.

Though we cannot explain the origin of orientation, it now seems clear that in the realm of molecular dimensions there is an orderliness in the growth of cells and parts of cells that can only be compared with the orderliness of crystal growth. We can begin perhaps to see, at the level of fine structure, how the shapes of cells and their component parts may be the expression of properties inherent in the molecules of which the system is composed. We recognize that certain of the substances synthesized by the cell tend to form ordered aggregates which, as Herzog saw, are the ultimate morphological units. It is suggested that the cell is constrained by these to assume a particular shape as it grows.

The value of the approach to biological systems through fine structure lies in that it provides, as Bacon would have regarded it, a corpuscular theory of living matter uniting morphology and physiology. Of the Democritan atomic theory, Bacon observed that it was either true or useful for the purpose of demonstration, for without positing atoms it is not easy to comprehend or to express in words the subtlety of nature (Bacon, 1653). Something similar may said of the approach through fine structure ; no previous approach has made it possible to regard shape and function, at certain levels of organization, as different aspects, in space and time, of a single type of organization.

It is perhaps in the ability of living substance to synthesize materials that tend to assume both an ordered texture and the external form of fibrils and laminae that the origin of shape in living systems resides. While it is sometimes convenient to think of the products of synthesis as separate from the living substance, they are not so in fact, but rather part of it ; and in that environment they can add to themselves or even participate, by virtue of their texture, in the synthesis of other parts—as do the chromosomes, for example.

Reading the title of this discussion one may well wonder what Goethe, who gave us at least the name of Morphology and was so hostile towards any analytical approach to biology—towards anatomy no less than chemistry (Goethe, 1807), would have made of such a conjunction. Perhaps he would have been less hostile towards a chemistry and physics largely peculiar to living organisms (he predicted a physico-chemical physiology) and largely comparative—as he recognized morphology must be. Of morphology he asserted that it seeks only to represent or demonstrate and not to explain (Goethe, *c.* 1795). Representation rather than explanation has been the intention of this account of the interrelation of shape and fine structure in cells and their parts.

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BIOCHEMICAL ASPECTS OF CELL MORPHOLOGY

By J. R. G. BRADFIELD.

It is well known that intricate structure exists within the protoplasm of living cells and the fact that biochemists can extract from this same protoplasm a remarkable array of complex organic substances is equally familiar. These substances, far from being haphazardly mixed, must be arranged within the cell in a very special way in order that their conflicting actions can be successfully co-ordinated. For this reason special interest attaches to the problem of fitting the proteins, polysaccharides, lipoids and nucleic acids of the biochemist into the mitochondria, Golgi droplets, nucleoli and chromosomes described by the cytologist. The importance of the problem was recognized long ago, but progress in solving it has been greatly hampered by the inadequacy of techniques available for studying ' biochemistry under the microscope '.

The kind of question which stimulates such investigations is this : if there were a complete list of all the substances present in a cell and of their metabolic relations, would it be possible to predict the protoplasmic structure which the cell would contain ? Fortunately or unfortunately this situation is unlikely to arise in the foreseeable future, but even with the very limited information available at present one is tempted to pose some such question, or its converse, i.e. given a particular histological or cytological structure of known function—a contractile vacuole, or a nerve or connective tissue fibre for instance—can one make predictions about its probable chemical composition ? Even in very specialized tissues such as nerve and muscle, which are in some ways the most favourable objects for such study, correlations of this kind are as yet very limited and in less obviously specialized cells, such as fibroblasts or liver cells, they are almost non-existent. Yet a fuller understanding of this aspect of living matter would be of great value in attempts to solve very different problems, such as the mechanism of organization or the physical basis of behaviour. The following discussion of a few special topics, concerning the interphase nucleus, the microsomes and mitochondria of the surrounding cytoplasm and finally the substances between cells, is necessarily brief. Where the facts seem to point distinctly in a particular direction it may be useful to speculate on their significance, since such speculation can in due course be tested experimentally.

The Interphase Nucleus.

The interphase nucleus has, so far, almost completely defied attempts to relate the intimate structure of its parts to their chemical constitution. The long filamentous chromosomes, which, except in their heterochromatic regions, are diffuse and difficult to distinguish in interphase nuclei, consist mainly of nucleic acids and proteins. Their major component is a complex of desoxyribonucleic acid and histone protein, but in addition they contain some ribonucleic acid and other non-histone proteins including the enzyme-protein alkaline phosphatase (Brachet, 1947 ; Willmer, 1942 ; Danielli and Catcheside, 1945 ; Mirsky, 1947 ; Ris, 1947 ; De Robertis *et al.* 1948 ; Bradfield, 1950). Molecules of desoxyribonucleic acid are known to have marked molecular asymmetry (Astbury, 1945) and to be capable of forming fibres very readily, which may be of importance in helping to maintain the fibrillar form of chromosomes. But as to how this desoxyribonucleoprotein complex is specially adapted to the dual function of exactly duplicating itself and of exerting a specific effect on the surrounding cytoplasm and hence on the whole organism we have no idea. A little is known about the physiology of the nucleolus, for it was discovered long ago that, especially in very rapidly growing cells, whole nucleolar buds may migrate into the cytoplasm (Wilson, 1925 ; Gresson, 1929, 1932). Relatively specific cytochemical studies by Caspersson (1947) and Brachet (1947) have shown that the cytoplasm in such cells, like the nucleolus, is very rich in ribonucleic acids. Migration of whole nucleolar buds is probably only an especially prominent instance of the diffusion of ribonucleoprotein from nucleolus to cytoplasm in all cells, varying in extent according to the amount of protein synthesis (Hyden, 1943) though it is not known whether the imprint of the genes is stamped upon this material, or whether they exert their specific influences in other ways. In addition to this transmission of material from nucleus to cytoplasm, substances must of course also pass in the reverse direction. Incorporation of radioactive phosphorus (which has been introduced via the blood stream) into rat liver nucleic acids is slow in the cytoplasm, but much more rapid in the nuclei—considerable quantities of phosphorus having passed through the cytoplasm and into the nucleus (Marshak, 1948). Because of this transfer of substances through the nuclear membrane, it may be expected that cell size will have an important effect on nuclear morphology since cell volume (and presumably the amount of material passing between nucleus and cytoplasm) increases as the cube of the radius, whereas nuclear area increases only as the square of the radius. Hence the remarkable labyrinthine nuclei found in the large cells of insect silk glands (Wilson, 1925, fig. 31) may be primarily adaptations providing increased nuclear area for exchange with the cytoplasm. Extremely convoluted nuclei might, however, prove an embarrassment in developing germinal cells, for these must remain capable of undergoing the mitoses which occur during subsequent development (where, incidentally, cell size and the ratio of nuclear volume to area are immediately reduced by cleavage without overall growth). It is noteworthy, therefore, that in many large oocytes the nucleus (germinal vesicle) remains spherical and is eased of its burden because abundant contributions of protoplasm rich in ribonucleoproteins pass directly into the egg cytoplasm from surrounding follicle cells. The latter, if large, possess highly convoluted nuclei (Wilson, 1925, fig. 320)—as if the oocyte nucleus had delegated this ingenious, but irrevocable, trick to the somatic follicle cells around it.

Consideration of the causes of such striking changes in nuclear shape is of considerable interest, but it deals only with the most superficial aspects of the main problem, for we know very little about the significance of the complex structure found inside nuclei. Let us therefore turn to the cytoplasm and see whether it is possible to trace there the ribonucleoprotein which, as mentioned above, passes out from the nucleus in many, if not all, cells.

Microsomes and Mitochondria.

In recent years attempts have been made to separate cell constituents in bulk by breaking down tissues in semi-physiological fluids and centrifuging the resulting suspensions (Bensley and Hoerr, 1934). Such direct attacks on the problem are fraught with considerable danger of artifact and for one reason or another most work has been concentrated on the very complex cells of mammalian liver. Nevertheless the results have been so consistent and in some cases so admirably quantitative that the conclusions drawn demand serious consideration. Cytoplasmic particles have been separated into two main groups—the large granules, varying from 0·5μ–2μ in diameter and consisting mainly of mitochondria and various secretory droplets, and the small granules or microsomes, which are not homogeneous, but range in size from 50–200 mμ. The greater the centrifugal force applied, the smaller the microsomes obtained and the richer they are in ribonucleic acid (Chantrenne, 1947), making it quite possible that they eventually lead back to, and arise from, this material rich in ribonucleic acid which is exuded from the nucleus. If this is so, they obviously occupy a key position in the cytoplasm and so it is not surprising to find that there is a good deal of evidence suggesting that they are, in fact, the main cytoplasmic site of protein synthesis—a most important metabolic process about which very little is known. Four pieces of evidence on this point may be mentioned briefly. First, it has been found that organs involved in protein synthesis, such as pancreas or silk glands, have abundant ribonucleic acid in their cytoplasm, whereas muscle or kidney which make little protein have relatively very little ribonucleic acid (Caspersson, 1947 ; Davidson, 1947). Microsomes are much richer in ribonucleic acid than any other cytoplasmic organelle—they contain about half of all that present in rat liver (Schneider, 1946), although they account for only 1/10th of the bulk of the tissue—and hence there is a strong likelihood that they are involved in the protein synthesis always associated with ribonucleic acid. Secondly, the very fine microsomes (and the ribonucleic acid-producing structures in the nucleus) increase markedly in liver tumour cells, which are synthesizing new protoplasm faster than normal liver cells (Price, Miller, Miller and Weber, 1949). Thirdly, if microsomes are the site of formation of new protein, one might expect to find in the cytoplasm a graded series of particles getting progressively larger and containing a progressively lower percentage of ribonucleic acid as more and more new protein accumulates in the particle, and there is some evidence that this is so (Chantrenne, 1947), though microscopic studies on this point are lacking. This view of things would suggest that the larger bodies in the cytoplasm may arise from these microsomes and hence it is interesting to note, as a fourth point, that when large granules are disintegrated in distilled water some of their contents dissolve completely, but some remain in the form of discrete granules about the size of microsomes, and these contain all the ribonucleic acid originally present in the large granules which were disintegrated (Claude, 1946).

It seems very probable, therefore, that the microsomes are the site of much of the protein synthesis that goes on in the cytoplasm. Hence it is not surprising that they contain only traces of the enzymes associated with liver metabolism (mostly oxidative enzymes have been examined), for these would only be in the process of formation in the microsomes. The large granules, consisting mostly of mitochondria, are, on the other hand, very rich in a variety of enzymes. There is a great deal of evidence indicating that they are the energy generators of the cytoplasm, producing the major part of the chemical energy required for cell metabolism. This view is based on the facts that, in rat liver, they contain almost all of the cytochrome oxidase, of the succinic dehydrogenase, of the enzymes of the Krebs dicarboxylic acid cycle, and of the enzymes involved in fatty acid oxidation (Hogeboom, Schneider and Pallade, 1949 ; Kennedy and Lehninger, 1948). There is not space here to describe the detailed action of these enzymes ; it suffices to say that together they account for a very large part of the complex cycle of enzymes necessary for extracting the energy from the sugar and fat which constitute the fuel of the cell machine and for transferring this energy to a special energy rich substance, adenosinetriphosphate (ATP). We may surmise, either that this ATP is passed like a fuel to the synthetic machinery of the cell, or else that it is used in the mitochondria to produce reactive precursor substances and that these are then passed to the synthetic machinery on the microsomes or elsewhere.

In case it appears that elaborate hypotheses have been erected around particles which may be entirely fictitious, it should be pointed out that methods of separation are being constantly improved and can now yield mitochondria very similar in shape and staining properties to those in the living liver cell (Hogeboom, Schneider and Pallade, 1949). Moreover, that the particles separated by bulk centrifugation are not the products of random disintegration is strongly suggested by their very constant composition and by recent work on the distribution of radioactive phosphorus in the particles (Jeener, 1949). Briefly, it has been found that the ratio of radioactive to total phosphorus is different and characteristic in each of the various fractions prepared by centrifugation of tissue suspensions from animals injected with radioactive phosphorus. This does not prove that the particles are identical with those in the living cells, but it does show that their phosphorus is not acquired by haphazard adsorption and that they do arise from different entities in the original cells. In passing it is interesting to note that the methods which give the best preparations of mitochondria yield microsomes which show marked birefringence when stirred or made to flow, indicating considerable asymmetry—either the individual microsomes are elongated, or they link together like rows of beads, and indeed the latter arrangement can be seen in electron micrographs of fibroblasts in tissue culture. In either case it is evident that in addition to their probable role in protein synthesis they may well play an important part in controlling the physical texture of the protoplasm.

As to what extent the morphology of these cytoplasmic constituents can be interpreted in terms of their chemical constitution, it is hard to say at present. However, it is clear from purely biochemical studies that elaborate cycles involving many enzymes are involved in the oxidative energy-producing metabolism of protoplasm and so it is not surprising that these should be concentrated in special bodies—the mitochondria—which are known to be surrounded by semi-permeable membranes and, at least in certain tissue culture cells, to undergo extensive movements through the cell, thus supplying all regions with the energy-rich, or specially reactive, products of their metabolism. The microsomes which appear to be concerned with protein synthesis are smaller and more numerous than the mitochondria. They are in fact of the same order of size as many virus particles and, like them, the smallest microsomes consist of little but nucleic acids and proteins and can form new protein when surrounded by the other constituents of an appropriate living cell. There may well be several kinds of mitochondria and microsomes in any one cell-type ; little evidence is available on this point. Nothing is known regarding the arrangement within mitochondria of the enzymes and nucleoproteins which they contain, but the arrangement of their other constituents has been discussed by Bourne (1942).

Collagen and Reticulin.

In conclusion, let us leave cell morphology and take at least one step toward a consideration of the morphology of the whole organism—namely by considering the loose fibrous connective tissue between cells. As yet little is known about the nature of the forces involved in morphogenesis, but at least the connective tissue fibres constitute the material basis through which these forces manifest their effects, the gross form of animals being largely determined by the nature and distribution of their connective tissue.

Neglecting the rather specialized elastic fibres, it is broadly speaking true that two main requirements are fulfilled by connective tissue fibres, and there are two main types of fibre, each specially suited to meet one of these requirements. First, there is the problem of providing mechanical strength, particularly important in tendons, skin and the capsules around organs. Thick, white bundles of wavy collagen fibres are found in such places. Secondly, there is the problem of ensuring plasticity—the ability to undergo rapid remodelling—particularly important in the connective tissue of embryos and of plastic tissues like lymph node, bone marrow and spleen. In this kind of situation we find the very fine reticular fibres, also known as argyrophil fibres because they are strongly and preferentially stained by silver solutions under certain conditions.

That these two kinds of fibre are very closely related is suggested by the way in which they follow each other in rapid succession in tissue culture and in the body (McKinney, 1930 ; Mallory and Parker, 1927). However, it is clear that the two are chemically different. Collagen is an almost pure protein containing very little carbohydrate and sulphur, whereas reticular fibres, although they consist mainly of a protein hardly different from that of collagen (Bowes and Kenten, 1949), also contain 2 per cent. sulphur and appreciable amounts of polysaccharides (of the general kind found in mucus and cartilage).

This is where the problem becomes interesting and also where facts end and speculation begins. Why is it that where plasticity is required connective tissue fibres are leavened with a pinch of polysaccharide ? An explanation seems possible in terms of what has gone before about the structural arrangement of the various metabolic processes within the cell. Consider the case of an embryo, slowly but continuously changing form throughout development. To ensure the necessary plasticity, the connective tissue cells must be able to loosen the reticular fibres to a more jelly-like consistency, stiffen them again, loosen them and so on, until the adult form is achieved and even then the process continues in plastic tissues like bone marrow and lymph nodes. It is known that cells can secrete enzymes capable of disrupting both proteins and polysaccharides into their smaller component units, but what of the reverse building-up process ? It has been pointed out above that protein synthesis very probably takes place in the microsomes and is necessarily an intracellular process, so that the fibroblasts would be unable to stick together the component units of the disrupted protein.* The polysaccharides present a very different picture, for, given glucose phosphate, a single enzyme, a phosphorylase, can build up the elaborate molecules of starch or glycogen in a test tube, and the same may well be true of the polysaccharides found in connective tissue. If this is so, it might be a relatively simple matter for the connective tissue cells to secrete the necessary factors which would re-form the giant polysaccharide molecules and hence rigidify the whole fibrous framework in question. Extensive experimental work on these and related problems has been carried out by Gersh and Catchpole (1950), in whose papers a more extensive discussion of the subject may be found.

It appears, therefore, that the mechanical demands of morphogenesis on the one hand, and the biochemical organization of cytoplasm on the other are responsible for some of the chemical characteristics of connective tissue fibres. It is, in fact, clear that at all sorts of points within cells and between cells there are intriguing possibilities of understanding the significance of form in terms of chemical composition or metabolic function and vice versa. It is unfortunately all too evident that knowledge in this field is most incomplete; nevertheless there is little doubt that a synthesis of this kind will eventually be achieved and that much of the intricate form within protoplasm will be explained in terms of 'fine structure'—in Dr. Picken's sense—and in terms of 'chemical geography'—to coin an expression covering the rather different aspect considered here. In so doing form is by no means 'explained away', but rather its interest and significance are raised above the somewhat empirical level at which they might otherwise remain.

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* It is sometimes possible for proteins to break into sub-units without rupture of peptide bonds, but collagen protein is not known to behave in this way.

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GENERAL DISCUSSION

Dr. G. H. Bourne : A great deal of the undergrowth which has obscured the Golgi problem for some years appears to have been cleared away by the work presented this afternoon by Dr. Baker.

In experiments which I have carried out, using a tissue disintegrator, mammalian liver cells have been examined at various stages of disintegration, both with and without the use of neutral red, and with subsequent staining on the slide with osmium tetroxide. The cells in the homogenate were examined by normal and by phase contrast microscopical methods and no trace of any structure resembling a network could be seen at any stage of disintegration of the cells. In the neutral red stained material large red droplets could be seen and a number of these stained black on the periphery when osmium tetroxide was run under the cover glass. In some cases these red droplets appeared to be surrounded by an osmiophil fluffy mass, and in one case two or three droplets were seen embedded in osmiophil material and attached to one side of an isolated nucleus. The osmiophil material may have been similar in origin to the myelin bodies which, according to Claude and Pallade, form as a result of the action of fixatives (including osmic acid) on some of the lipoid containing neutral red globules in the cell. This work appears to confirm Dr. Baker's results, and if we also accept the work of Pallade and Claude it becomes very difficult to regard the Golgi net as anything but an artifact—regrettable as this conclusion may be to many cytologists and not least to me.

I should also like to comment upon a subject introduced by Dr. Bradfield, that is, the structure of collagen and pre-collagen or ' reticular ' fibres.

If you take a strip of hexagonal net and stretch it, the folded ends of the hexagons give a cross-banding appearance to the strip. Collagen fibres also show cross-banding when examined under the electron microscope ; and it is suggested that the expanded network in which the sides of the hexagons are made up of protein micelles, is the form taken by the pre-collagen fibres ; and that the stretched network is the form of the mature collagen fibre. Such an arrangement would explain the ready interconvertibility of collagen and pre-collagen and if we assumed that the interstices of the network in the pre-collagen fibre were filled with mucoid material (not a very extravagant assumption) and that this mucoid material was squeezed out when the hexagons closed we get an explanation of the chemical difference between pre-collagen and collagen fibres, for this mucoid material contains both a carbohydrate and a sulphur component, both of which are present only in greatly reduced amounts in collagen, but which are present in much larger amounts in pre-collagen fibres.

Dr. C. Helen Brown : The more highly oriented the protein molecules in a biological structure are, the less probable is their arrangement. Orientation can only be maintained provided that inter-molecular forces are holding the molecules in position. Often these are electrovalent forces, such as salt links and hydrogen bonds, which develop between the side chains or the back bones of adjacent protein molecules. Such linkages are influenced by changes in pH + ionic content of the medium, and give relatively soft structures, often containing much water, and are suitable only for protein structures formed inside the animal. When proteins are used on the outside of terrestrial animals, or to form hard resistant structures, chemical bonding between the molecules is found. In the invertebrates this is generally quinone bonding, while in the vertebrates it is cystine bonding, though quinone bonding occurs in the egg cases of Selachian fishes.

Mr. M. Pryor : Dr. Picken has pointed out that it is not always possible to account for the molecular orientation of a structure as being the effect of simple physical causes, such as turgor pressure. This is particularly true of what I may call functional orientation, in which the molecular arrangement confers on the material directional properties useful for its working. As an example of a purely functional orientation we may consider a man-made structure such as the fuselage of the ‘ Mosquito ’ aircraft. The grain of the plywood makes an angle of 45° with the long axis ; an arrangement that in a plant cell we should call a ‘ crossed spiral ’. This arrangement confers maximal torsional stiffness, but makes it easy to bend the wood to the curvature of the tube in construction. The same arrangement is found in the skin of sharks and many teleosts, where similar conditions apply ; the crossed spiral permits of maximum flexibility in bending so that there is no interference with swimming, and at the same time may allow the skin to contribute to the torsional rigidity of the trunk. No one would suggest that the orientation of a dogfish skin was due to turgor pressure. In the pupal cocoons of *Donacia* on the other hand there is a similar arrangement which almost certainly is so caused ; each case must be judged on its merits.

Decision is made more difficult by the fact that we do not really know what type of orientation to expect from the action of any given set of forces. It is often said that chain molecules tend to align themselves parallel to the direction of maximum tension, but this is only true of a particular set of conditions ; flexible molecules united into a three-dimensional network. For more rigid molecules not firmly attached to one another we should expect orientation along lines of shear, which would produce an entirely different pattern. Many more experiments on high polymers of known constitution are needed before we can work out what to expect in any particular case.

Dr. PANTIN replied : When I suggested that this discussion would disclose in fine structure a new system with morphological rules of its own, I think you will agree that I spoke correctly. Dr. Baker has shown us something of the real nature of intracellular systems. Dr. Picken has shown us something of the relation of their morphology to molecular structure. Mr. Bradfield has shown us something of the relation of the chemical geography of the cell to its metabolic processes. The subsequent speakers have made abundantly clear that they are already in a position to attempt to interpret structure in terms of complex molecular models with the properties of which they are familiar. Nevertheless we are only beginning to understand the rules of this morphology—much as men in the 18th century were only beginning to understand the rules of gross morphology.

[*Paper read in title at the General Meeting on 9 March 1950* :]

A NEW METHOD FOR THE IDENTIFICATION AND STUDY OF CRITICAL GROUPS

By A. J. WILMOTT

The identification of ‘ critical ’ species, that is, those closely allied species which differ in their diverse combinations of small differences rather than in the possession of features peculiar to each species, has increasingly become work for the specialists. The method to be described here should enable any careful student to make accurate identifications without a long preliminary study of the critical group, once that group has been well described by a specialist, and the resulting descriptions set out in accordance with this new scheme.

At present the specialist by long study has to store in his memory as many as he can of the various combinations of small differences by which the members of the group—whether termed species or subspecies is immaterial—are distinguished. He simplifies his task by regarding some differences as more important and others as of lesser value. It is doubtful whether he is ever able to achieve a mental picture of all the characters of each of the species. The new method aims at making a presentation of all the differences so that a truer picture of them all can be perceived.

It is easily established, if not already well known, that the normal process of thought, in which words are used to connote concepts of all kinds, is a slow one. Its maximum speed is apparently that at which nerves can transmit separate impulses, viz., about 10 per second. This can be established if one tries to enumerate verbally as quickly as possible objects visible to the eye, such as table, chair, book, paper, pen . . . Four, or sometimes five, can be done (by me) at about 10 per second, and then the mind becomes a blank. But the 'eye' can perceive impressions at a greater rate, and habitually does so when two or more closely allied species are seen side by side, for one can often say immediately, 'This is different from that', without any formulation of the differences which exist. The method here set out aims at making it possible to compare the summation of differences instead of adding up the separate differences one by one in sequence. The differences must in this method be set down one by one, but in such a way that in the end their sum-totals can be compared.

For explaining the scheme I have here chosen as an example the British representatives of the genus *Euphrasia*, because they have been described on a uniform plan by Pugsley in 'A Revision of the British *Euphrasiae*' (1930: *Journ. Linn. Soc., Bot.*, **48**, 467–544, pls. 26–37), and in 'Notes on British Euphrasias'—III–VI, in the *Journal of Botany*, 1933–1940.

In the diagrams, one line of squared paper is devoted to the variation in the genus (in the British Isles) of a single feature of the plant; length of stem, stoutness of stem, direction of stem growth, colour of stem, indumentum of stem (four lines), length of internodes, etc., etc., detailing the characters of habit, stem, foliage, inflorescence, flower and fruit. In this example twelve variants of each, when as many as this are required, have been distinguished, and one square (1–12) allotted to each variation of each feature. Each of the species distinguished by Pugsley has a separate diagram, the variation within each being shown by blacking in the squares corresponding to the characters of the particular species. In this way a distinctive diagram is obtained, representing the characters dealt with, for each. Some selection has been made from the descriptions as the squared paper used did not permit the representation of all the features described by Pugsley, but this is immaterial for the purpose of explaining the scheme. If more features were to be set out, smaller squares could be used, or a second diagram provided for features believed to be of lesser importance in identification, however important they may be for the full study of the group. If true specific differentiae should exist, peculiar to the species, these can be stated apart from the diagrams, as these are primarily intended to set out the combinations of characters which occur in several or many of the species.

The 36 features used in the diagrams are lettered A to Z (omitting J, O and U) and a to p (omitting i and j), and the variations of each numbered 1–12, according to the lists given below. For identification all that is necessary is for the student to make from his specimen (preferably series of specimens in a critical group) a similar diagram from these lists of variations of features, and compare it with the published diagrams until the blackened squares coincide. The student's diagram would be best on translucent paper which could be superimposed on the printed diagrams. This would require that the printed diagrams should have squares of such a size that squared paper of similar mesh is available for the use of the student: if this cannot be done the student would first have to transcribe the printed diagrams on to paper available for his use. Comparison will probably be easier if the diagrams of plants for identification are made by inserting dots in the appropriate squares instead of blacking them out, as blacking out obscures the underlying diagram with which comparison is bring made.

If no diagram is found to fit that prepared by the student from his specimen, it will be probable that the variation of the nearest fit is actually wider than has been described, and the knowledge of the variation of that form will be increased. If the diagram does not nearly fit any of the printed diagrams it is probable that the student has before him a new member of the critical group. In either case the value of the diagrams for study of the group will be evident.

It should be added that in drawing up variation lists, the classes should as far as possible be based on absolute differences, e.g. on measurements rather than in terms of ‘ large ’, ‘ small ’, etc. Existing descriptions are not well suited to the method of study here suggested.

To do this for *Euphrasia* would, however, involve a new monographic study to replace ‘ slenderness ’ and ‘ robustness ’ by diameters of stem or some objective data, and similarly with various other features described by Pugsley. Correspondence with Dr. E. O. Callen, who showed interest in the scheme and offered at my request suggestions for modification, showed that to make modifications would involve a great deal of further work on the genus. As the diagrams are here offered primarily as an example, it seemed best to leave the diagrams based on Pugsley's *Monograph*, although with his descriptions it is not always possible to arrange the categories 1–12 into a regular series, which should be the aim of those using this method.

For purposes of mere identification it has been suggested that the system of scheduling variation in separate variables might be better applied by using punched cards and selecting implements, such as the Copeland-Chatterson Paramount Sorting System. With the selector one could, certainly, pick out the card with which any specimen registered from the same schedule agreed. But the use of such a method would presuppose that all the species were rightly described and registered, and that all the variation was known. If no card emerged which exactly corresponded with a scheduled collection the student would not know where the discrepancy had occurred. It might be due to some error in registration, or to some extension of the known variation, or to the discovery of a new species. And it would not be easy to discover which. But on the system here suggested this would not occur.

From a comparison of one diagram with another the main agreements and discrepancies stand out. It would be possible to form a reasonable opinion as to the nature of the discrepancy, and the standard diagrams would be modified in the light of study until they more accurately represented the variation of the various species.

Indeed, the system should be a valuable aid to the study of variation as such. If series of 9 (or 16 or 25 or more) specimens of a supposed single species are registered from a number of localities, by placing in each suitable square a dot for each specimen in a definite position, e.g.

1	2	3
4	5	6
7	8	9

1	2	3	4
5	6	7	8
9	10	11	12
13	14	15	16

1	2	3	4	5
6	7	8	9	10
11	12	13	14	15
16	17	18	19	20
21	22	23	24	25

the variation in each locality could be registered and that in different localities compared. It would be possible to see how far there was differential local variation. The similar study of supposedly hybrid populations might give interesting results, and the comparison of such diagrams from many localities should show what variation is probably due to hybridization and what is mere intraspecific variation. Further, such diagrams would show whether there is correlation between various characters.

I would again emphasize that the *Euphrasiae* are used merely as an example of the proposed method. If due allowance is made for the fact that the schedule from Pugsley's data is not entirely suitable for use with the method, I think it will be found that by its use it is possible to identify collections of *Euphrasia* from the diagrams given here, in spite of discrepancies which will be sure to be found owing to the relative unsuitability of some parts of the schedule. The correct way to make the schedules of the separate variables in critical groups will be discovered as the method is used and the actual variation from locality to locality becomes better known in consequence. It is, however, believed that the method should prove a useful tool in the hands of the serious student of variation in critical groups.

In testing these diagrams I have found it possible to make identifications which are completely confirmed by comparison of my material with specimens in the herbarium so named by Pugsley, although I had no special previous knowledge of the genus. I found, however, considerable discrepancies between the diagrams prepared by me for identification and that prepared from Pugsley's descriptions with which my diagram seemed most similar. Others will certainly find similar discrepancies, which are partly due to ignorance whether Pugsley would have called the green 'deep' or 'dark', the corolla lines 'fine' 'distinct', 'well-marked' or 'strong', and so on. In such cases I put a '?' in each of the possible squares, as understanding of Pugsley's terminology can sometimes come only after considerable study. This emphasizes the necessity of using absolute differences in the preparation of schedules for the application of this method. But other discrepancies were also found, and later, after comparison with herbarium specimens named by Pugsley, discovered to be due to the incompleteness or inadequacy of Pugsley's descriptions. Thus immediately the value of the method showed itself, as it led to improvement of the monographer's description: it was not the method that was at fault, but the descriptions. When diagrams have been prepared from natural populations, using an improved schedule, such discrepancies will not occur unless the population registered is an unusual one. In order to minimize the discrepancies which will be found, and to complete diagrams when Pugsley's descriptions are incomplete, I have filled in certain squares with vertical/horizontal cross-hatching, using for the purpose herbarium specimens named by Pugsley. The diagonally cross-hatched squares indicate variations stated by Pugsley to be less usual or uncommon.

The best way of preparing the diagrams so as to emphasize their differences has yet to be found by experience. Various alternatives have been considered. It may be that it would be better to black out all squares regardless of the frequency of the variation, and to cross-hatch or stipple all the squares between the black squares and the base-line on the right of the diagram. This might make more 'solid' looking diagrams more readily distinguished by the eye, but the possibility of indicating normality and less usual variants would be lost. This would be disadvantageous if is practicable to indicate different frequencies of variation by different forms of cross-hatching. Experiment with the method will reveal the best form of diagram—possibly different forms for different purposes. The essence of the novelty lies in the avoidance of the necessity of mentally registering differences one by one, by the use of a second spatial dimension as opposed to a linear tabulation of any kind. Further, bias in comparison is eliminated because one does not know (until after long use, perhaps) what the discrepancy signifies until the schedule has been consulted. It is not possible to put greater weight on one or other character until much registration of actually existing variation has been made. When extra weight can be given to certain characters on the basis of diagrams prepared from natural populations, it will then have a factual basis, and will not be dependent on the possible bias of a monographer. When the relative worthlessness—from a systematic standpoint—of a certain feature has been demonstrated by diagrams of natural populations, it can be omitted from a later edition of the schedule. By that time, however, the variation will be much better known than it is at present.

The varieties and forms distinguished by Pugsley have here been indicated by letters placed in the appropriate squares, as the preparation of separate diagrams for each—which may be preferable for study—would involve much further investigation. The present paper shows how the method can be adapted for use with existing descriptions. With schedules prepared *ad hoc* for study *ab initio* the diagrams produced should prove much more satisfactory.

Since the above was written it has occurred to me that the difficulty of obtaining thin paper with squares of the same size as the figures can be overcome by providing a blank diagram as a figure of the same size. As a background behind thin paper it can be used for the registration of series collected for study.

The present method has been developing in my mind for some twenty-five years, but I was unable until 1946 to satisfy myself as to the most generally useful method of presentation. Furthermore, my friend Miss Brenhilda Schafer has drawn my attention to a similar method tried out not long ago by industrial psychologists, in attempting to correlate the requirements of jobs with observed data from tested applicants. It was not pursued as the results were not good. Their conclusion was that the method was not good ; my own conclusion would be that the psychological presumptions were unsound. The method should prove good if the psychological requirements for particular jobs were rightly estimated.

Schedule of Characters and their Variation

A. Length of stem, in centimetres.

(1) 1 ; (2) 2 ; (3) 4 ; (4) 6 ; (5) 8 ; (6) 10 ; (7) 12 ; (8) 15 ; (9) 20 ; (10) 25 ; (11) 30 ; (12) more than 30.

B. Stem stoutness.

1. Slender
2.
3. Rather slender.
4. Medium ; neither slender nor robust.
5.
6. Rather robust.
7.
8. Moderately robust.
9.
10. Robust.
11.
12. Very robust.

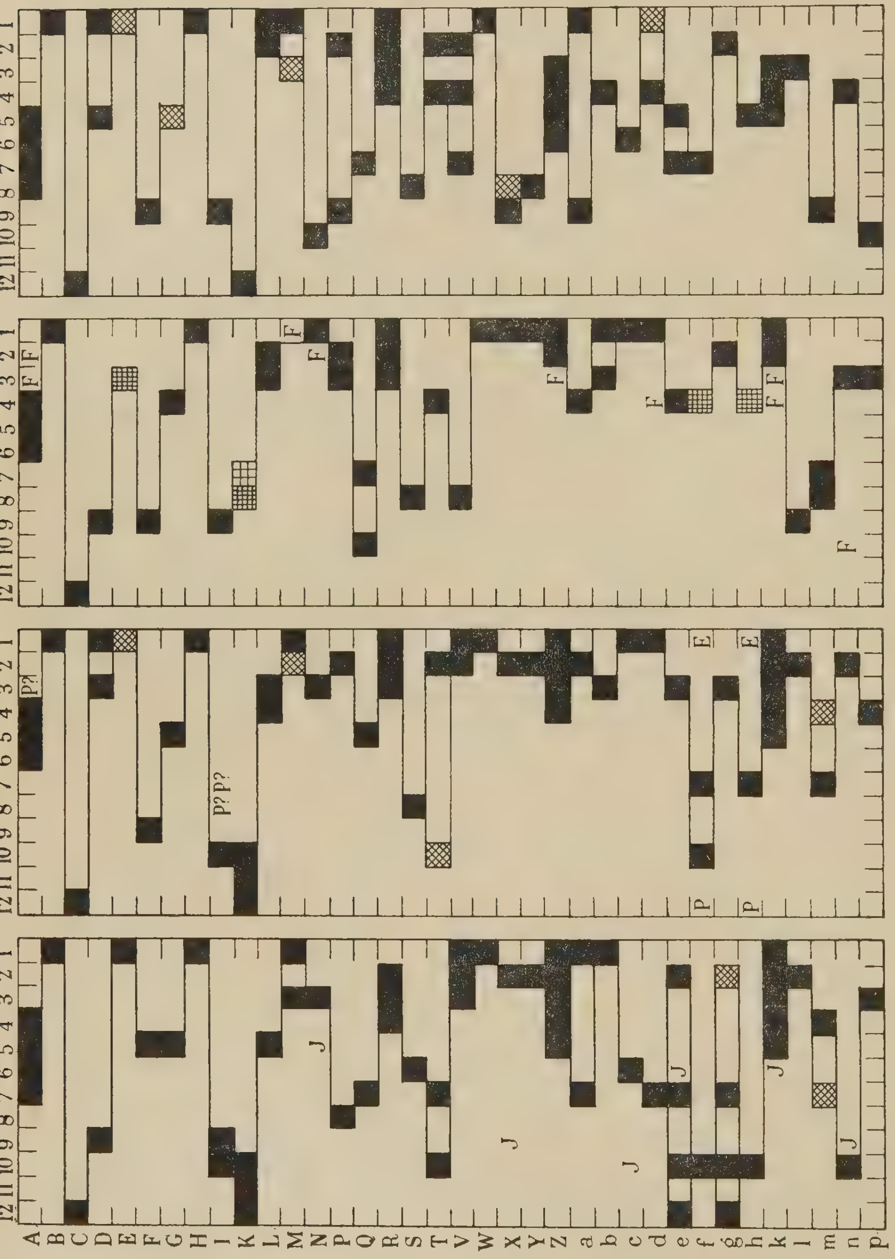
C. Stem direction.

1.
2. Decumbent.
3.
4. Ascending from decumbent base.
5.
6. Ascending.
7.
8. Suberect from decumbent base.
9.
10.
11.
12. Erect.

D. Stem colour.

1. Green.
2. Greenish.
3. Tinted with red or dull red.
4. Slightly red
5. Reddish.
6.
7.
8. Tinted with purple.
9. Purplish.
10. Purple.
11. Violet.
12. Dark violet.

Fig. 1.



1. *E. micrantha* Rchb. J.—var. *Johnstoni* Pugsl. The f. *simplex* Pugsl. is not separable on the diagram.

2. *E. scotica* Wettst. E.—f. *estriata* Pugsl. P.—var. *purpurascens* Pugsl.

2 (2). *E. rhumica* Pugsl. F.—var. *fonchrensis* Pugsl.

3. *E. frigida* Pugsl.

E. Stem hairs (all said to be 'crisped').

1. Fine short.
2.
3. [Shortish].
4.
5.
6. Stout bristles.
7. Variable in length.
8. Longish.
9.
10. Long.
11.
12. Coarse.

F. Stem hairs : direction.

1.
2.
3. [Some somewhat spreading].
4.
5. Spreading.
6.
7. Spreading and longer above.
8.
9. Deflexed.
10.
11.
12.

G. Stem hairs : density.

1. None.
2. Fewish.
3.
4.
5. More or less dense.
6.
7. Dense at (or to) base).
8.
9. Dense towards top.
10.
11. Dense all over.
12.

H. Stem glands.

1. None.
2.
3. Occasional about upper nodes.
4.
5. Some (variable in length) in upper part.
6.
7. Often with longer (than eglandular hairs) glandular hairs above.
8.
9. Regularly with longer more spreading glandular hairs above.
10.
11.
12.

I. Stem internodes.

1. All short and contracted (plant dwarf).
2. All shorter than the leaves, but not 'contracted'.
3. Lower contracted : upper longer than leaves, but not 'elongate'.
4. Lower contracted : upper elongated.
5. Lower about equalling the leaves : upper shorter than leaves.
6. All about equalling the leaves.
7. Lower moderately longer than the leaves : upper shorter than the leaves.
8. All moderately longer than the leaves.
9. Lower elongate (much longer than the leaves) : upper shorter than the leaves.
10. Lower elongate : upper less elongate.
11. All elongate.
12. All very elongate.

K. Inflorescence internodes.

1. All contracted in dense imbricated spike.
2. All shorter than the bracts, in densish spike.
3. All shorter than the bracts, in laxish spike.
4. All shorter than the bracts, in lax spike.
5. Lowest longer than (or subequalling) bracts, but most shorter, and spike densish.
6. Lowest longer, but most shorter, and spike laxish.
7. In lower half longer than the bracts : upper half of spike densish.
8. In lower half longer than the bracts : upper half of spike laxish.
9. In lower part longer than the opposite (or subopposite) bracts : top of spike densish.
10. In lower part longer than the opposite (or subopposite) bracts : top of spike laxish.
11. In lower part longer than the alternate bracts : upper part densish.
12. In lower part longer than the alternate bracts : upper part laxish.

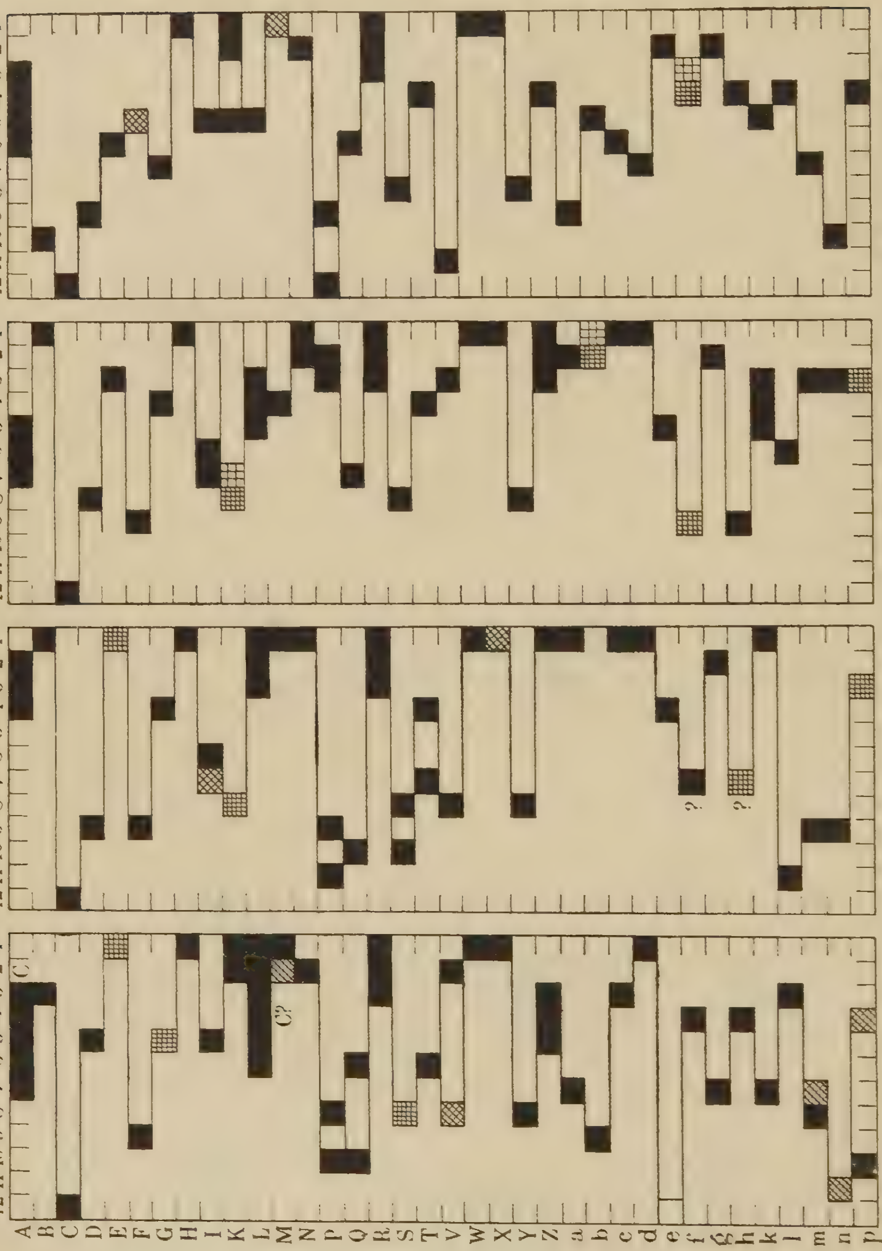


FIG. 2.

4. *E. foulaensis* Towns. C.—**f. *condensata* Pugsl.** M.—**var. *maritima* Pugsl.**

4 (2). *E. eurycarpa* Pugsl.

4 (3). *E. Heslop-Harrisoni* Pugsl.

5. *E. rotundifolia* Pugsl.

L. Node from which flowers begin : nth node above cotyledons. n.=
1. 2 or 3.
2. 4.
3. 5.
4. 6.
5. 7.
6. 8.
7. 9.
8. 10.
9. 11.
10. 12.
11. 13.
12. 14 or more.

M. Branches.
1. None.
2. Few : from the base or near the base.
3. Few : from mid-stem (upper flowerless leaf axils).
4. Several : from base or near base.
5. Several : from midstem.
6. Numerous : starting from base or near base.
7. Numerous : starting from about mid-stem.
8.
9.
10.
11.
12.

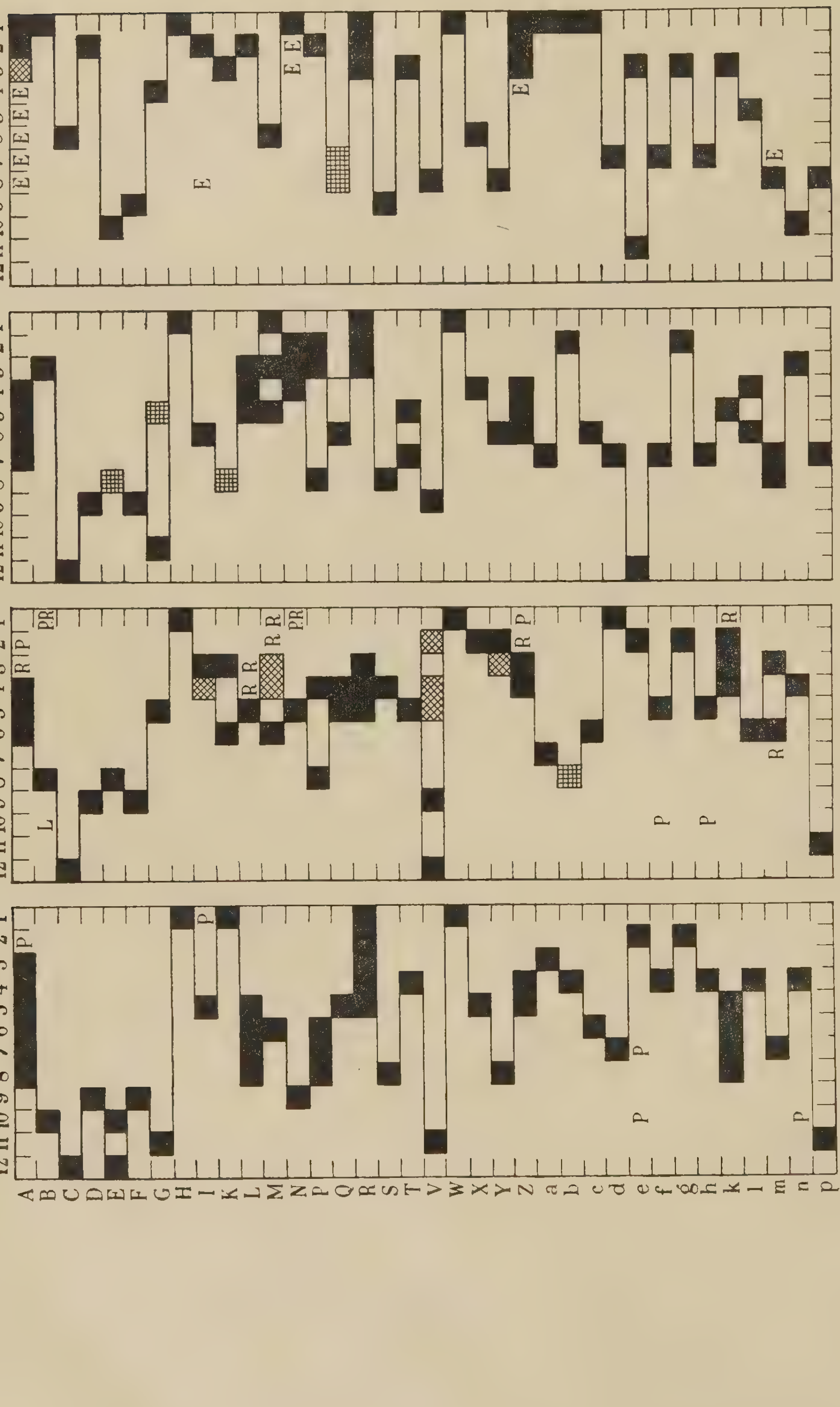
N. Leaves (cauline) : length. [Pugsley only gives the length of the largest : diagrams need amplification from specimens.]
1. 5–6 mm.
2. 7.
3. 8.
4. 9.
5. 10.
6. 11.
7. 12.
8. 13.
9. 14.
10. 15.
11. 16.
12. 17 and over.

P. Upper cauline leaves : shape.
1. Narrow (linear, oblanceolate, or narrowly oblong).
2. Oblong.
3. Oblong-obovate.
4. Narrowly ovate.
5. Ovate.
6. Obovate.
7. Rhomboidal.
8. Oval.
9. Broadly oval or broadly ovate.
10. Broadly obovate.
11. Roundish ovate.
12. Orbicular.

Q. Cauline leaves (upper) : apex.
1. Acuminate.
2. Acute.
3. Subacute.
4. Acutish (angle greater than 90 degrees).
5. Obtuse.
6. Very obtuse.
7. Rounded obtuse.
8. Rounded.
9.
10. Truncate.
11.
12.

R. Upper cauline leaves : number of teeth each side.
1. 1.
2. 2.
3. 3.
4. 4., etc.
6. 5.

FIG. 3.



6. *E. Marshallii* Pugsl. P.—var. *pygmaea* Pugsl.

7. *E. curta* (Fr.) Wettst. L.—f. *littoralis* Pugsl. P.—var. *piccola* Pugsl. R.—var. ***rupestris*** **Pugsl.**

7 (2). *E. Campbellae* Pugsl.

8. *E. cambrica* Pugsl. E.—f. *elatior* Pugsl.

S. Cauline leaves (upper) : shape of leaf teeth.

1. Aristate.
2. Acuminate.
3.
4. Acute.
5.
6. Acutish (subacute).
7.
8. Obtuse.
9. Obtuse and shallow (‘ crenate ’)
10. Very obtuse.
11. Flattened obtuse.
12.

T. Cauline leaves : colour (upper side ; under side paler in some species).

1. Yellowish green.
2. Light green.
3. Bright green.
4. Dull green.
5. Greyish green.
6. Deep green.
7. Dark green.
8.
9. Tinted with reddish or brown.
10. Tinted with purple.
11. Tinted with dark red or dark purple.
12.

V. Cauline leaves : hair indumentum.

1. None : leaves glabrous.
2. Leaves glabrous except for minute bristles on margins only.
3. Leaves glabrous except for minute bristles on margins and nerves beneath.
4. Subglabrous except for minute bristles on margins only.
5. Subglabrous except for minute bristles on margins and nerves beneath.
6. Subglabrous on surface but with longer hairs or bristles on nerves beneath.
7. Upper surface with minute bristles.
8. Both surfaces hirsute (or pubescent) with longer hairs or bristles.
9. Both surfaces ; and longer hairs on nerves beneath.
10. More or less densely hirsute and longer hairs on nerves beneath.
11. More or less with short and longer hairs on both surfaces.
12. More or less with some long hairs.

W. Glands on cauline leaves.

1. None.
2.
3.
4.
5.
6. Minute on nerves beneath.
7.
8. Short-stalked glands.
9.
10. With longer and shorter glands on both sides.
11.
12. With dense long and short glands, especially beneath.

X. Calyx teeth.

1. Short (triangular) acute.
2. Short (triangular) finely acuminate.
3. Short (triangular) subulate.
4. Short.
5. Rather long : subacute.
6. Rather long : acuminate.
7.
8. Long, finely pointed.
9. Long, finely acuminate.
10.
11.
12.

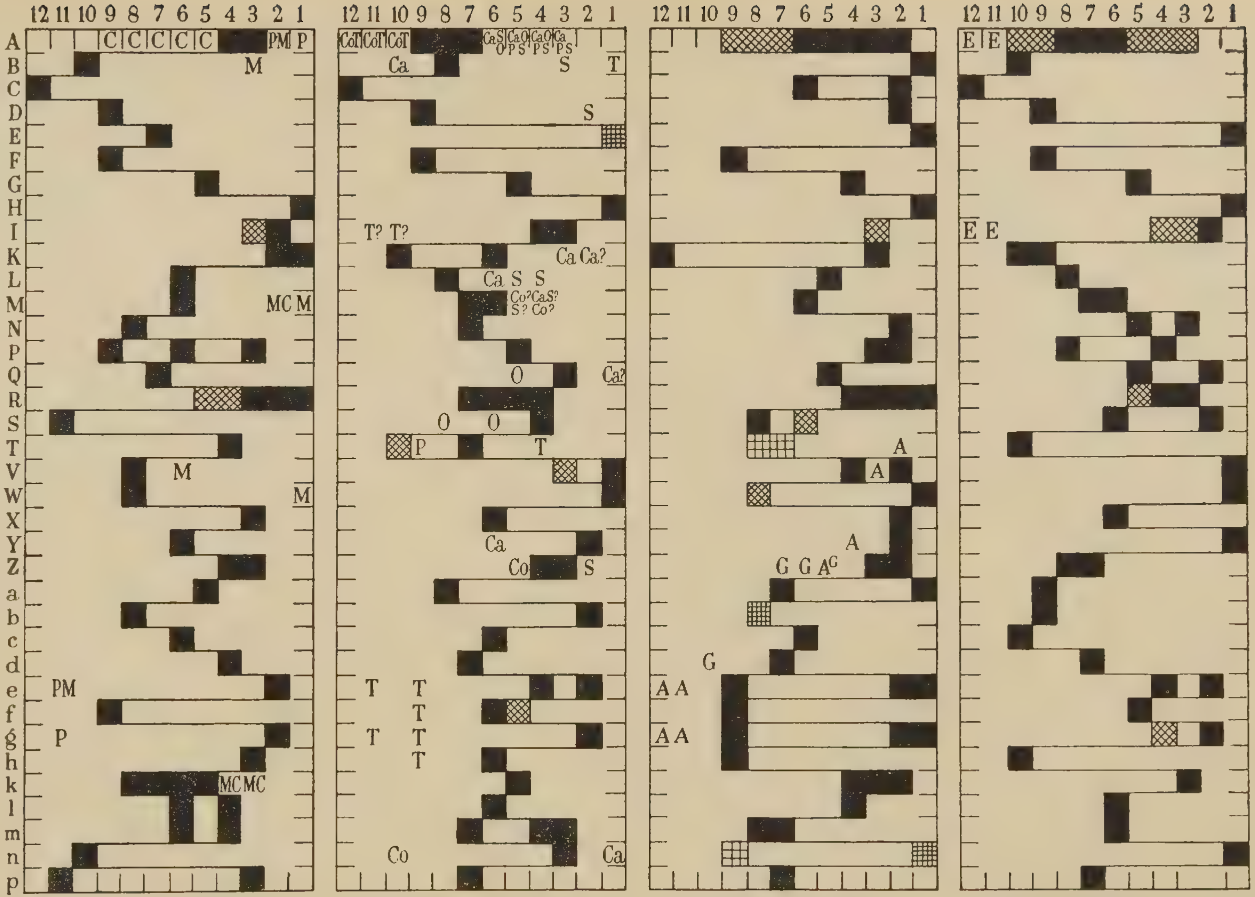
Y. Calyx accrescence in fruit.

1. Not accrescent.
2. Scarcely accrescent.
3. Scarcely accrescent, but inflated.
4. Slightly accrescent.
5.
6. Somewhat accrescent.
7.
8. Accrescent in fruit.
9.
10. Strongly accrescent.
11.
12.

Z. Corolla : dorsal length. (in millimetres). [*E. Rostkoviana* and *E. montana* elongate during anthesis.]

1. 4.
2. 4·5.
3. 5.
4. 6.
5. 7.
6. 8.
7. 9.
8. 10.
9. 11.
10. 12.
11. 13.
12. 14 or more.

FIG. 4.



9. *E. occidentalis* Wettst.
P.—var. *praecox* Bockn.
M.—var. *minor* Pugsl. C.—var. *calvescens* Pugsl.

10. *E. nemorosa* (Pers.) Löhr.
Ca.—var. *calcarea* Pugsl.
Co.—var. *collina* Pugsl.
S.—var. *sabulicola* Pugsl.
T.—var. *transiens* Pugsl.
P.—f. *procumbens* Pugsl.

11. *E. confusa* Pugsl. A.—var. *atroviolacea* Pugsl.
G.—f. *grandiflora* Pugsl.

12. *E. pseudokerneri* Pugsl.
E.—f. *elongata* Pugsl.

a. Corolla : lobes of upper lip.

1. Subentire.
2.
3. Denticulate.
4.
5. More or less retuse.
6.
7. Retuse.
8. Notched.
9. Emarginate.
10.
11.
12.

b. Corolla : lobes of lower lip.

1. Narrow.
2. Rather narrow.
3. Median lobe narrow.
4. Median lobe narrower than laterals.
5.
6.
6.
8. Rather broad.
9. Broad.
10.
11.
12.

c. Corolla : relative lengths of upper and lower lips.

1. Lower lip scarcely exceeding upper.
2.
3. Lower lip rather longer than upper.
4.
5.
6. Lower lip longer than upper.
7.
8.
9.
10. Lower lip much longer than upper.
11.
12.

d. Corolla : lobes of lower lip.

1. Subequal.
2.
3.
4. Middle lobe rather longer than laterals.
5.
6.
7. Middle lobe longer (not ' much longer ') than laterals.
8.
9.
10. Middle lobe much longer than laterals.
11.
12.

e. Corolla : colour (excluding the dark lines) : upper lip [lower lips same : see ' g '].

1. More or less yellow.
2. White.
3. Whitish.
4. Bluish.
5. Light blue.
6. Lilac tinted.
7. Lilac.
8. Purplish lilac.
9. Purplish.
10. Purple.
11. Violet tinted.
12. Violet.

f. Corolla : lines (more or less purple) on upper lip. [lower lip see ' h '.]

1. None.
2. Faint.
3. Fine.
4. More or less ' distinct '.
5. ' Distinct '.
6. ' Marked ' (not strong).
7. More or less ' marked '.
8. Well marked.
9. More or less strong (? = ' dark ').
10. Strong.
11.
12.

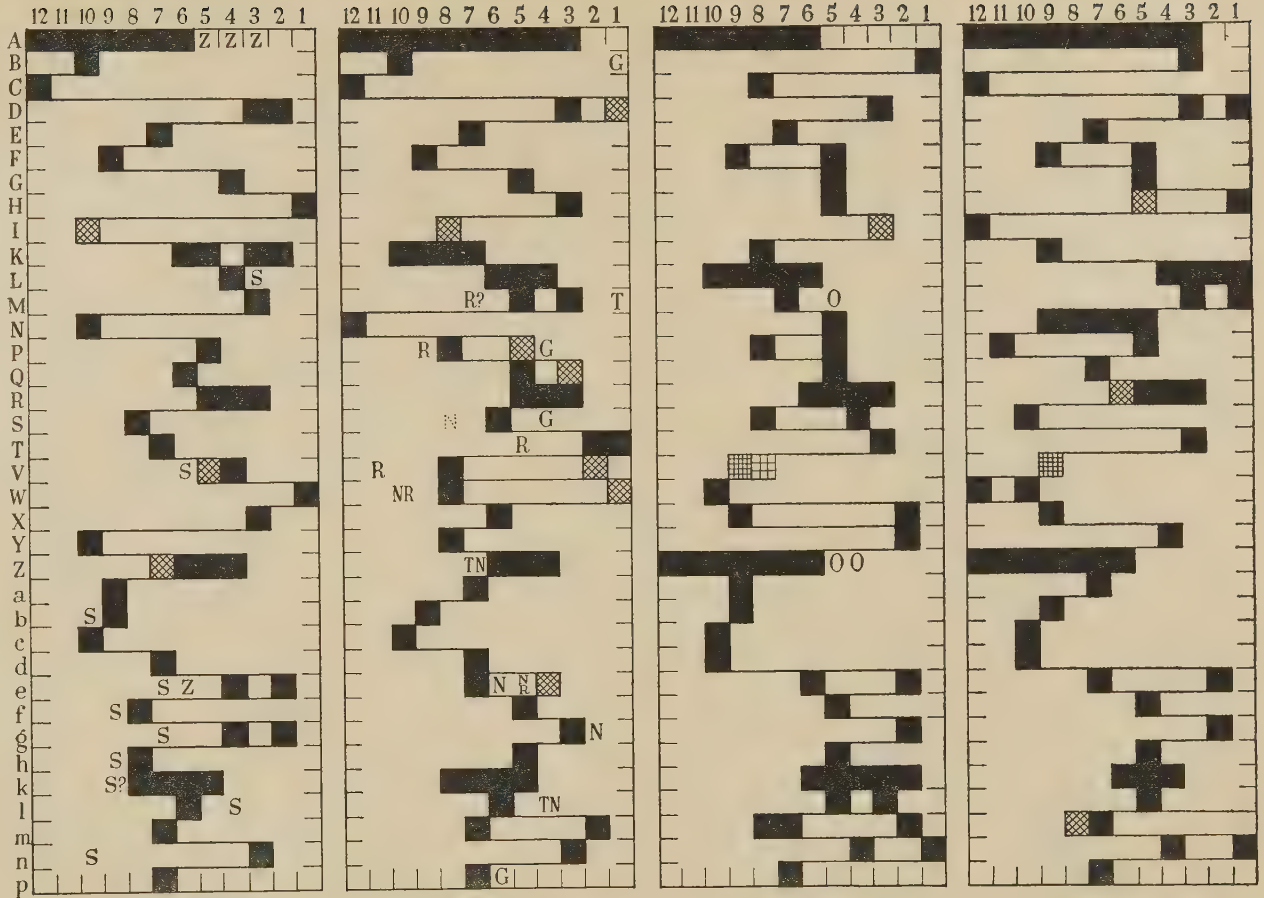
g. Corolla colour : lower lip. 1–12 as ' e '.

h. Corolla : lines on lower lip. 1–12 as ' f '.

k. Capsule length : in millimetres.

1. 4.
2. 4·5.
3. 5.
4. 5·5.
5. 6.
6. 6·5.
7. 7.
8. 8.
9. 9.
10.
11.
12.

FIG. 5.



13. *E. borealis* Wettst. Z.—var. *zetlandica* Pugsl. S.—var. *speciosa* Pugsl.

14. *E. brevipila* Burn. & Greml. G.—f. *gracilius* Pugsl. T.—f. *tenuiformis* Pugsl. N.—var. *notata* Pugsl. R.—var. *reayensis*

15. *E. Rostkoviana* Hayne. O—var. *obscura* Pugsl.

16. *E. montana* Jord.

l. **Capsule shape.**

1. Linear oblong.
2. More or less narrowly oblong.
3. Elongate elliptic.
4. Oblong elliptic.
5. Elliptic.
6. Oblong.
7. Broadly elliptic.
8. Oblong ovate.
9.
10.
11.
12.

m. **Capsule : apex.**

1.
2. Rounded.
3. Rounded truncate.
4. Truncate.
5. Subtruncate.
6. Slightly retuse.
7. Retuse.
8. Emarginate.
9. Deeply emarginate.
10.
11.
12.

n. **Capsule length relative to calyx teeth.**

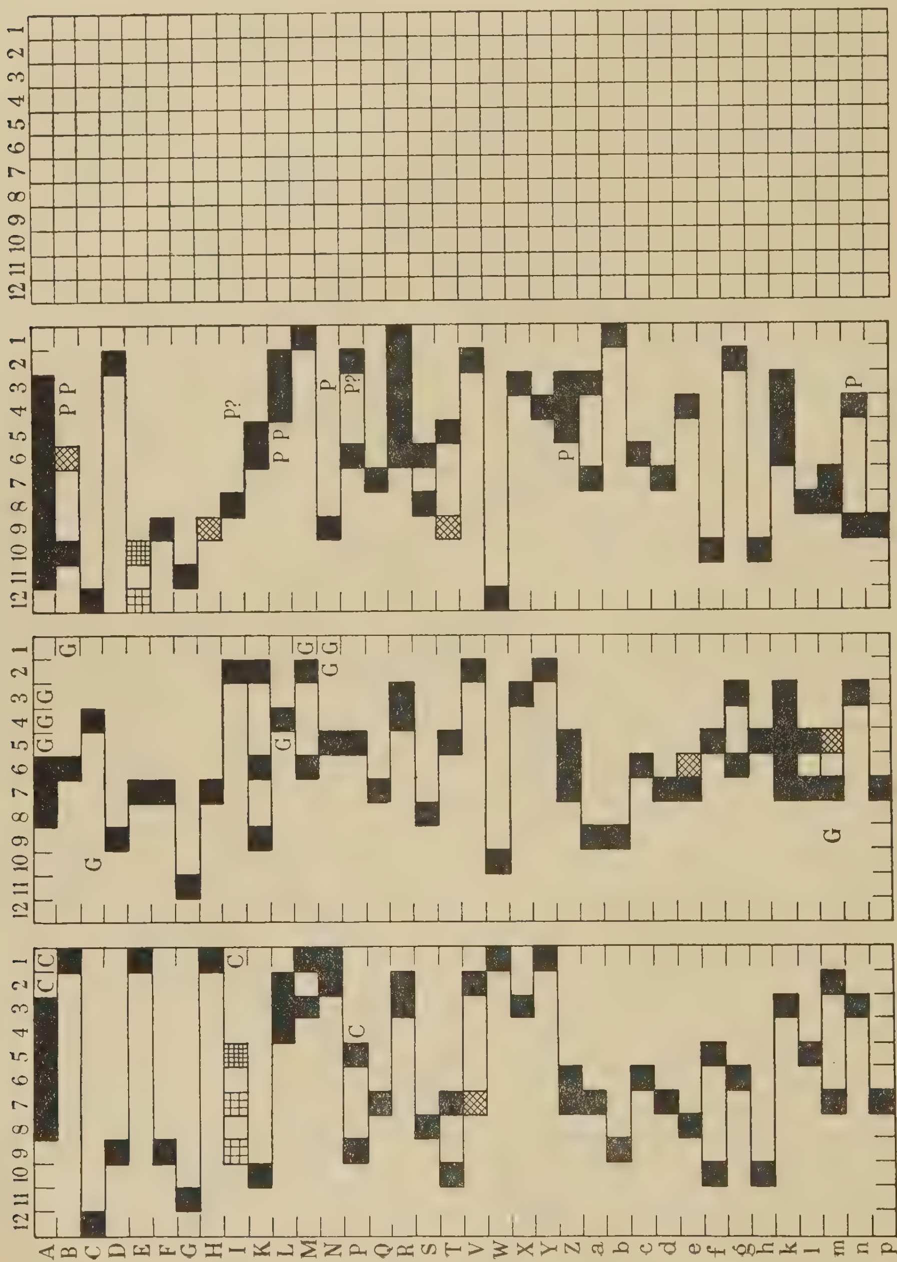
1. Shorter.
2. Not exceeding.
3. Subequalling.
4. Equalling.
5.
6.
7.
8.
9. Slightly exceeding.
10. Exceeding.
11. Much exceeding.
12.

p. **Capsule : indumentum** (in 3–12 the margin is ciliate).

1. Glabrous.
2. Subciliate with a few weak bristles.
3. Glabrous except for the marginal ciliae.
4. Nearly glabrous.
5.
6.
7. Slightly (sparsely) pilose.
8. Shortly pilose.
9. Subpilose.
10. More or less pilose distally.
11. Pilose distally.
12. More or less pilose all over.

The diagram of *E. salisburgensis* Funck has been omitted to make room for the blank for the use of students. Its narrow leaves with long sharp arrect teeth make it easily recognizable from all other British species.

FIG. 6.



17. *E. rivularis* Pugsl. C.—f. *compacta* Pugsl.

18. *E. anglica* Pugsl G.—var. *gracilescens* Pugsl.

19. *E. hirtella* Jord. P.—var. *polyadena* (Gren. & Rouy) Pugsl.

OBITUARIES

Stephen John Batchelder was born in Great Yarmouth, 31 May 1870. His father who bore the same Christian names, Stephen John, was well-known in East Anglia as a painter in water-colours of Broadland scenery, his pictures being exhibited at Norwich, Ipswich, and elsewhere. Mr. Batchelder received training for the teaching profession at St. John's College, Battersea, and eventually became science-master at the Ipswich higher grade schools under the Ipswich Education Committee. He was a Fellow of the Royal Horticultural Society and delivered courses of lectures on botany and horticulture under the Ipswich Technical Instruction Committee, which has now ceased to exist. He was one of the founders of the Ipswich Field Club which after its amalgamation with the Ipswich Science Gossip Club is now called the Ipswich and District Naturalists' Society, and for many years he acted as guide in their botanical forays where his extensive knowledge of the Suffolk Flora made his services invaluable. But Batchelder had other interests beside those of nature study, and the beautifully illuminated Addresses he produced for presentation purposes and for use in his Masonic Lodge are evidence that he inherited some of his father's artistic instinct. For several years before his death he was collecting material for a treatise on ' Floral design in Mediaeval Architecture ' but this work was unfortunately never completed. His last contribution to local botanical knowledge was a report on ' Wild plants growing on waste ground in Ipswich ' which was published in the *Transactions of the Suffolk Naturalists' Society* (1949), of which body he was a valued member. He was elected a Fellow of the Linnean Society in 1928. He died at his home in Belle Vue Road, Ipswich, on 9 November 1949, leaving a widow and two daughters. The funeral took place on the 14th at the Ipswich Crematorium. A. MAYFIELD.

Professor **Walter Garstang** who died on 23 February 1949, at the age of eighty-one, was one of the outstanding personalities of British Zoology for more than half a century. Not only was he a pioneer in marine biology, and one of the founders of fisheries research, he also made fundamental contributions to zoological theory.

The eldest son of Dr. Walter Garstang of Blackburn, he was born on 9 February 1868, and educated at Blackburn Grammar School and Jesus College, Oxford. He came up to the university with a scholarship in 1884, when only sixteen and half years of age, intending to read medicine. At heart he was a poet and a lover of nature. A new world opened before him as he came under the influence of that great naturalist H. N. Moseley who was then the Linacre Professor ; he very soon decided to abandon his medical studies and join the honours school of Zoology. He was only twenty when he took his degree and had the distinction of being appointed to the original staff of the Plymouth Laboratory when it opened in 1888 just after he had graduated. He was appointed to be an assistant to the first director, G. C. Bourne, and so at once his career became bound up with the development of marine biology in this country. In 1891 he went for a year to Manchester to be Berkley Fellow of the Owens College and returned to the Marine Biological Association at Plymouth as Assistant Naturalist. In 1893 he was elected a Fellow of Lincoln College and to a Lectureship in 1894 ; so for a time he returned to Oxford and was there when Ray Lankester was in the Linacre Chair. But in vacations he continued to work at Plymouth, and in these early years he wrote many papers on the morphology, bionomics and distribution of marine invertebrates. He was particularly attracted to the Nudibranch molluscs and did pioneer experiments to test and confirm the hypothesis of their warning coloration. He began his researches on the Tunicata, the group to which he was to return in later life ; and it was in this period too that he published his delightful studies on the habits and respiratory mechanisms of the sand-burrowing crabs.

His life's work may be divided into three periods: the first occupied with these many and various researches in pure marine biology; the second devoted to fishery investigations; and the third, when a university professor and in retirement, occupied with more fundamental problems in Zoology and his poetic interpretations of bird song.

The second period began in 1897 when he went back once more to the staff at Plymouth; this time as Naturalist in charge of Fishery Investigations. He became the moving spirit in the development of fishery science in England. He was clearly much impressed by Johan Hjort's pioneering research in Norway and his first paper in this period was an extensive account of Hjort's methods. Like Hjort he planned his work on a wide front and soon he was publishing papers on such different aspects of fisheries work as 'The Surface Drift of the English Channel and Neighbouring Seas during 1897', 'On the Variation, Races and Migration of the Mackerel' (1898), 'On the Plankton and Physical Conditions of the English Channel' (1899) and on 'The Impoverishment of the Sea' (1900). Great things were astir of Oceanography at the turn of the century; in 1899 the King of Sweden invited all the countries interested in the fisheries of the North Sea and adjacent waters to send representatives to Stockholm to a conference to discuss the possibilities of collaboration in a programme of marine research. A second conference was held, this time in Christiania, in 1901, and to this Garstang went as a delegate of His Majesty's Government; this was the conference which set up the International Council for the Exploration of the Sea. Each country participating undertook to investigate a particular region of sea and different problems in fishery research so that, as time went on and their results came in, the whole area would be covered and all the bits of research fit together as part of one great plan. The different nations equipped their separate research vessels and marine laboratories.

The English and Scottish fishery departments were then, as is still the case to-day, separate institutions; and the Fishery Board for Scotland had already begun its investigations well before the end of the century. The English department, a small branch of the Board of Trade as it was then, commissioned the Marine Biological Association to start its research for it as part of the international scheme; so it was that Garstang became Director of these investigations and established a laboratory at Lowestoft. With his assistants William Wallace, R. A. Todd and George Atkinson, and the famous old research trawler *Huxley* he carried out from Lowestoft those classical investigations into the natural history of the North Sea plaice which have laid the foundations of English fishery research. By extensive age determinations and measurements and particularly by liberating vast numbers of marked fish at different points (to be returned when recaught by fishermen) he studied the natural growth rates and migrations of the fish in different areas. He realized how overcrowded the young plaice were on the nursery grounds off the Dutch coasts and how much more food there would be available for their growth on the Dogger Bank; he tried the experiment of transplantation. He caught and marked large numbers of young fish on the coastal banks; half of these he returned to the sea where he caught them and the rest he carried in tanks of seawater to be released on the Dogger Bank. When in time the marked fish were recaught it was found that those taken to the richer feeding grounds had in two years grown twice as big as those left behind. Garstang had pointed the way to a farming of the sea, but he was before his time. In his Buckland Lectures in 1929 he returned to the subject and showed how such a transplantation on a large commercial scale could be made to pay, the increased yield of fish giving an ample margin of profit over the estimated cost of transport; but no nation was likely to undertake the cost of this, for all other nations would be free to reap the reward. While the nations work together in the science of the sea, the days of their co-operation in its exploitation are still far in the future;

but one day surely the North Sea will be farmed in the way that Garstang showed—let us hope that his name will be remembered.

In all these early years, with Hjort, he played a prominent part in the development of the International Council ; from 1902 to 1908 he was scientific adviser to the British Delegates and convener of the International Committee on Trawling Investigations. In 1906 he was awarded his Oxford D.Sc.

Garstang was an individualist, a lover of freedom and independence, who resented what appeared to him to be government interference in his scientific programme when official policy did not coincide with his own plans. At the same time as the newly constituted government Fishery Department decided in 1907 to take over the investigations from the Marine Biological Association he received a letter inviting him to accept the Chair of Zoology at the University of Leeds. It was a difficult decision for him to make ; on the one hand he loved his marine work, on the other he felt he would never be happy if he was not entirely free to shape his own policy. Very reluctantly he resigned from his Directorship at Lowestoft and, on becoming Professor Garstang, the third phase of his life began. In passing it may be said that he regained a connexion with this work in 1919 when he was appointed a member of the Development Commission Advisory Committee on Fishery Research, on which he served till the end of the recent war.

For a time his output of research was much reduced. He had all his lectures to prepare ; he was building an honours school of zoology where none had existed before ; and he was making himself a terrestrial naturalist instead of a marine one. Insects and birds became the objects of his field studies. It was at this time that his love of nature and his strong poetic feeling led him to delight in the study of bird song which he later interpreted in verse and music in a little book *Songs of the Birds* which went through several editions.

After nearly twenty years of marine work he came back to more academic zoology and took up again the study of those problems which had fascinated him when he was an undergraduate at Oxford in the heyday of speculation as to the evolutionary origin of the different groups of animals. The main trends of zoological interest had in the meantime flowed into the fields of more experimental and genetical work, and by the time he came to publish his morphological and embryological speculations, now into the 1920's, they were considered by many as out of date. Nevertheless in this, for the time being unfashionable field, he made contributions to his science of outstanding and lasting value. In his essay on ' The Theory of Recapitulation ' which he read before the Linnean Society in 1921 (published in the *Journal* the following year) and in his presidential address to Section D of the British Association in 1928, he put forward his revolutionary views on the influence of modifications in development upon the course of evolution. With them he helped to overthrow the influence of Haeckel's so-called ' Biogenetic Law ' which had dominated zoological thought for so long. Gavin de Beer followed him in 1930 with his masterly *Embryology and Evolution* which in its second edition was renamed *Embryos and Ancestors*. Garstang coined the term *paedomorphosis* to apply to the evolutionary influence of larval characters upon adult organization ; in contrast de Beer placed alongside it the term *gerontomorphosis* to cover those phylogenetic effects which were produced by the modification of characters already present in a line of adults.

The writer remembers a remarkable lecture on ' Larval Forms ' that Garstang gave in 1920 to the students attending the Easter Class at the Plymouth Laboratory. In this he discussed the question as to whether the planktonic larval stages of marine invertebrates represented a primitive ancestral pelagic adult type, as so many at that time thought, or did they represent special larval (caenogenic) adaptations ? He left one in no doubt that the second view was correct. With rapid sketches on the board he made a brilliant survey of the larvae of the many different groups and showed how in each there was a compromise and adjustment between two rival needs—or in other words two competing selective advantages: on the one hand to grow up into the adult and reproduce the species, and on the other to distribute the species far and wide in the ocean currents (particularly important in species with sedentary adults). He showed clearly how the larval stages were as much adapted for dispersal as were the seeds or fruits of rooted plants; but he showed how in all manner of different devices in different groups those two rival ' needs ' were met. In his British Association address he developed this theme together with his ideas of paedomorphosis. He showed the likely adaptive advantage to the larva of the remarkable torsion which suddenly develops in the young gastropod veliger and how this in consequence has come to be so striking a feature of adult gastropod anatomy.

It is a great pity that he never wrote the book he often planned to put his many original ideas on larval adaptations, paedomorphosis and phylogeny in straight prose; instead he used to give his views in lighthearted verse for the amusement of his zoological friends and students. Seeing these ideas decked out in comic dress, many people, I think, failed to realize that Garstang really regarded them as having profound significance. As an example I cannot resist quoting the first part of his ' Ballad of the Veliger, or How the Gastropod got its Twist ':

The Veliger's a lively tar, the liveliest afloat,
A whirling wheel on either side propels his little boat;
But when the danger signal warns his bustling submarine,
He stops the engine, shuts the port, and drops below unseen.

He's witnessed several changes in pelagic motor-craft;
The first he sailed was just a tub, with a tiny cabin aft.
An Archi-mollusk fashioned it, according to his kind,
He'd always stowed his gills and things in a mantle-sac behind.

Young Archi-mollusks went to sea with nothing but a velum—
A sort of autocycling hoop, instead of pram—to wheel 'em;
And, spinning round, they one by one acquired parental features,
A shell above, a foot below—the queerest little creatures.

But when by chance they brushed against their neighbours in the briny,
Coelenterates with stinging threads and Arthropods so spiny,
By one weak spot betrayed, alas, they fell an easy prey—
Their soft preoral lobes in front could not be tucked away!

Their feet, you see, amidships, next the cuddy-hole abaft,
Drew in at once, and left their heads exposed to every shaft.
So Archi-mollusks dwindled, and the race was sinking fast,
When by the merest accident salvation came at last.

A fleet of fry turned out one day, eventful in the sequel,
Whose head-and-foot retractors on the two sides were unequal:
Their starboard halliards fixed astern ran only to the head,
While those aport were set abeam and served the foot instead.

Predaceous foes, still drifting by in numbers unabated,
Were baffled now by tactics which their dining plans frustrated.
Their prey upon alarm collapsed, but promptly turned about,
With the tender morsel safe within and the horny foot without!

* * * * *

Many of Garstang's friends and former pupils have expressed a wish that the best of these verses should be published in a small booklet ; the writer hopes shortly to carry out this idea.

In 1928, the same year as his British Association address, he published his great paper on 'The Morphology of the Tunicata, and its bearing on the Phylogeny of the Chordata '*. In this, besides a host of points bearing on the evolution of the Tunicates and lower Chordates, he put forward in greater detail the idea he tentatively suggested in a paper in 1894 ; that the Chordates were derived by paedomorphosis from the pelagic larval form of sedentary invertebrates and that the Ascidians were not degenerate Chordates, as was usually held, but lived as the ancestors of the group must have lived sending up pelagic larvae which took to swimming to prolong their planktonic life. This is such an important contribution to zoological theory that I feel it should be emphasized by a quotation from Professor de Beer's appreciation of it in his *Embryos and Ancestors* (pp. 52–54):

' Garstang was the first to look for the trace of the ancestors of the vertebrates in early instead of adult stages of invertebrates ; and he focused his attention on the larvae of Echinoderms (starfish, sea-urchins, sea-cucumbers, etc.). He showed that if the ciliated bands on the larva (auricularia) of a sea-cucumber were to become accentuated and rise up as ridges leaving a groove between them, and if these ridges were to fuse, converting the groove into a tube, a structure would be produced which has all the relations of the vertebrate nervous system, including such details as the neurenteric canal. Not only this, but the two modifications of the vertebrate nervous system which are found in *Amphioxus* and all higher forms on the one hand, and in sea-squirts on the other, can be based on differences which are found in the disposition of the ciliated bands on different kinds of Echinoderm larvae. This theory of the origin of the vertebrate nervous system has several advantages. In the first place it avoids the difficulties which beset any attempt to derive it from the existing nervous systems of any other invertebrate. It also agrees with the principle of neuro-biotaxis, according to which a concentration of nervous tissue takes place in the region of greatest stimulation. If the ancestors of the vertebrates had crawled about on their ventral surfaces like most invertebrates, one would expect their nervous system to be ventral, like that of most of the invertebrates. But the nervous system of vertebrates is dorsal, and it is precisely the dorsal side of the body which would receive the greatest stimulation in a form swimming freely in the sea, the stimuli being the rays of light penetrating through from the surface. Not only is the auricularia free-swimming, but it bears an unmistakable resemblance to the tornaria larva of *Balanoglossus*, and *Balangoglossus* is an undoubted relative of *Amphioxus* and the early vertebrates (or chordates as they may more correctly be termed). But the resemblance between the Echinoderm larva and the chordate goes further still, for the former has an adoral ciliated band formed partly from the inner layer of the body ; and in a corresponding position the chordates have a ciliated band called the endostyle, which is looped in the same peculiar manner as the other. The middle layer of the body arises in three tiers or segments in the Echinoderm larva and in *Balanoglossus*, and indications of this tripartite arrangement are present in *Amphioxus*. Further, the body-cavity of the Echinoderm larva is in communication with the outside by a pore, as in *Balanoglossus*, *Amphioxus*, and several other chordates. In fact, if the nervous system and endostyle are formed in the way suggested, all that is required to turn the Echinoderm larva into a chordate is the formation of the notochord and the piercing of the gill-slits '.

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* *Quart. Jour. Micr. Sci.* **72**, pp. 51–187.

Scarcely less important is his large paper on ' The Morphology and Relations of the Siphonophora ' published in 1946,* only two years before his eightieth birthday. For more than a century two opposing views as to the nature of the siphonophores have had many advocates : the ' poly-organ or medusome hypothesis ' and the ' poly-person or swimming hydroid-colony hypothesis '. Garstang reviewed the evidence for each and made a detailed study of the many different accounts of siphonophore morphology and bionomics : he did not favour either view—but came to a new and original interpretation which might perhaps be called the ' Actinula hypothesis '. He believed that the siphonophore colony had arisen by paedomorphosis—by the precocious development of a still floating larval polyp form of some original hydroid stock : a larval form comparable with the actinula larva of Tubularia.

It must I think be admitted that a number of his other ideas were regarded by many zoologists as too speculative—and built upon rather slender evidence. His love of phylogenetic speculation unfortunately made some people hesitate to consider seriously his more carefully worked out ideas ; nevertheless these two large papers, on the Tunicata and Siphonophora, are, I believe, assured of a place as classics in zoological literature. His attack upon Haeckel's Biogenetic Law and his opposition to some aspects of official policy in fishery matters, undoubtedly brought him into conflict with some of the more influential zoologists of his day. It is only fair to say that if he had to fight, he thoroughly enjoyed it.

He was a great teacher who by his infectious enthusiasm filled his pupils with a love of zoology ; he was also their friend. He delighted in taking part in student activities : he took a prominent part in the University Officers Training Corps ; he formed the Leeds University Boat Club, and he wrote and produced *The Student's Opera*—a parody on Gay's immortal work. I cannot do better than quote from the obituary notice written in *Nature* by Professor L. Eastham, one of his former pupils :

' Few who go from us will leave behind so much affection and such a sense of gratitude. It is inevitable that his students will remember Garstang for his perpetual youth and his genial kindness. They will think of their visits with him to the marine station which he established at Robin Hood's Bay ; of teas in the laboratory at which he and Mrs. Garstang were generous hosts and at which the week's problems were discussed ; and of their open house at Meanwood where all students were welcome '.

There was yet that other important side of his personality ; his strong poetic feeling which partly found expression, as already stated, in his studies of bird song, but in addition provided a large number of poems of which only a few were published. Among the latter I may mention ' The Song of the Tree Pipit ' (*The Times*, 8 May 1919) ; ' The Return to Oxford : a Memorial Lay ' which was a long poem published by Blackwell of Oxford in 1919 describing his thoughts on visiting Oxford just after the war, and seeing the young men returning—in it he mourned the death of his zoologist friends and former companions at Oxford : Geoffrey Smith, Wilfred Jenkinson, Arthur Darbishire, Edward Minchin and George Grosvenor ; ' To a Herring Gull ' (*The Oxford Magazine*, 6 February 1920), and ' Friendship ' (*Nature*, 7 July 1921). Then there were his essays ' Wordsworth's Interpretation of Nature ' which was published as a special supplement to *Nature* (16 January 1926), and ' Wordsworth's Green Linnet ' (*Nineteenth Century*, September 1929).

After his retirement Oxford became the home of the Garstang family, and here he continued his researches and writing up to the very end. On his eighty-first birthday, and less than a fortnight before he died, he went up to London to take part in the special symposium on Bird Song at the Linnean Society.

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* *Quart. Jour. Micro. Sci.* **87**, pp. 103–193.

His very happy life and biological interests were shared by Miss Lucy Ackroyd, of Newnham College, whom he married in 1895 ; she died in 1942, and they are survived by a son and five daughters. A. C. HARDY.

Miss **Ida Margaret Hayward**'s main contribution to Botany was the great share she had in the preparation and publication of Hayward and Druce's *The Adventive Flora of Tweedside*, which appeared in 1919 and attracted much attention in many centres, commercial as well as botanical, throughout the world. But further reference to the book should be preceded by some explanation as to the reasons which led Miss Hayward to devote so long a period of her life to this task.

She was born at Trowbridge, Wilts, in 1872. Both sides of the family were connected with the cloth industry. One grandfather was a West of England manufacturer, while the grandfather on the mother's side was engaged in the woollen trade at Galashiels in Scotland. On her father's death she came with her mother to reside in Galashiels, where two of her brothers were connected in business with woollen mills belonging to their uncles—the firm of Messrs. Sanderson. One of these uncles, William Sanderson, was a keen observer. Apart from the difficulty which was caused by the presence in imported wool of very troublesome prickly fruits and seeds, he was attracted by the way in which many of the fruits and seeds survived the drastic treatment which was necessary to free the wool from these encumbrances. In spite of the high temperatures of the process and the use of acids, it was observed that many of the seeds survived this treatment and were able to germinate, whereas others succumbed. These experiments of Mr. Sanderson are referred to in some detail in the *Adventive Flora* (page xx). Miss Hayward had already taken a good deal of interest in the native flora and in botany generally, and it was Mr. Sanderson who first suggested to her that an investigation into the aliens of the Tweed area might be well worth her study. These aliens were at that time particularly prevalent, as large quantities of wool were being brought in from Australia, New Zealand and South America. The refuse from the mills was carried down the river Gala as well as to many other parts of the Tweed and its tributaries. The number of seeds which survived the cleaning process, germinated, and produced flowering plants, was very considerable. It was fortunate that Miss Hayward began her work when she did. Later on considerable changes were made in the cleansing processes, with the result that in recent years few seeds have been scattered and the alien flora has for the most part disappeared. Miss Hayward made a most exhaustive survey and at the time the only comparable work carried out on such a profusion of aliens was that done at Montpelier. There the work of several botanists was brought together by Dr. Thellung of Zürich in the classic entitled *La flore adventice de Montpelier*. The aliens of the Montpelier collection did not bear much similarity to those collected by Miss Hayward, as the French manufacturers then used wool drawn from sources other than the countries which provided the material for the Border industry of Scotland. The large collection made by Miss Hayward would not have received adequate examination and publication had it not been for the fortunate co-operation of Dr. Claridge Druce, who in his turn invoked the aid of Dr. Thellung. The identification of the material coming from many isolated countries necessitated the aid of many botanists at home and abroad, to whom Dr. Druce paid tribute in the Preface to the book. The result justified the long period of time which Miss Hayward devoted to it and is also a tribute to the work done by Dr. Druce, to whom fell the chief responsibility of identication and editing. Miss Hayward's collection was in Dr. Druce's opinion a unique one at the time in respect to numbers. The main body of the work is prefaced by a very able Introduction from Dr. Druce's pen. The few pages of this Introduction contain much of interest and well deserve re-reading. The general text is no mere list of aliens but contains many observations worthy of record. The book is well illustrated and one might call particular attention to figure 77, where the power of penetration shown by the fruits of *Hordeum murinum* through the actual skin of the sheep is very well shown. The very special herbarium on which the book is based was given by Miss Hayward shortly before her death to the Royal Botanic Garden, Edinburgh, where it is preserved.

As already indicated, Miss Hayward's work on the aliens came almost to an end when the process of cleansing the wool was completely altered. Subsequently she was more concerned with the natural history of the Border countries. She, however, did a good deal of travelling, visiting various parts of the world, including South America and South Africa. By this time she had taken keenly to photography and to coloured films. During her visits abroad she secured some excellent records of botanical subjects which later she had the pleasure of exhibiting. In her final years she spent most of her time illustrating in colour the scenery and plants of the Scottish Borders, and particularly during the war was a very popular lecturer in the Border towns where she had many enthusiastic audiences. In this way she was able to raise considerable sums of money which she devoted to local charities.

After the publication of the *Adventive Flora of Tweedside* Miss Hayward had the opportunity of making exhibits of the more interesting aliens to various societies, including the Linnean Society of London and the Botanical Society of Edinburgh. Her films were also exhibited to the Royal Scottish Geographical Society and, as late as 1948, to the Botany Section of the British Association at Dundee.

She was elected a Fellow of the Linnean Society in 1910 and had a long connection with the Botanical Society of Edinburgh, becoming a Fellow in 1913.

Her death took place after a brief illness at Galashiels on 2 October 1949.

WILLIAM WRIGHT SMITH.

Paul Marchal (1862–1942) a été certainement l'un des meilleurs zoologistes de sa génération. Il a consacré toute sa vie à la recherche scientifique et ses travaux resteront classiques. La précision des résultats et l'élégance simple de la forme y sont constamment associées. Il s'est révélé presque immédiatement comme un chercheur pénétrant par le choix même de l'objet de ses recherches et l'importance des constatations qu'il y réalisait. Cela lui valut d'être, dès 1912, élu membre de l'Académie des Sciences. La notice (Notice sur les Travaux, scientifiques de M. Paul Marchal, Paris, 1912, 138 pp., 65 figs.) sur ses travaux, qu'il a, suivant un usage qu'on ne saurait trop approuver, publié à cette occasion, reste la meilleure source pour embrasser l'ensemble de son oeuvre à la période la plus feconde. J'en résumerai ici les données les aspects et essentiels.

Dès ses premières publications sur les instincts des Sphégides paralyseurs (*Arch. zool. expérim,* ser. ii, **65**, 1887), son sens précis de l'expérimentation biologique se manifeste et bientot ses thèses de doctorat en médicine (1890) et ès sciences (1892) le font nettement émerger parmis les jeunes hommes de son âge. Le second de ces mémoires a pour sujet l'anatomie et la physiologie de l'appareil excréteur des Crustacés décapodes. Mais désormais il se consacrera complètement à l'étude biologique des insectes et ses publications s'y succéderont nombreuses et pleines d'intéret. Je ne puis ici que retenir les principales. Je citerai d'abord son magnifique mémoire (1896) sur la reproduction et l'évolution des guêpes sociales où il met en évidence la castration nutriciale des ouvrières.

Attaché en 1894, comme chef de travaux pratiques, à la Station entomologique nouvellement créée a l'Institut agronomique, puis professeur dans la chaire de Zoologie de cet établissement (1898), toute sa carrière s'y déroulera et ses recherches combineront harmonieusement les problèmes pratiques d'entomologie appliquée à la défense des cultures contre les insectes nuisibles et l'étude des questions les plus variées et les plus élevées de la biologie générale.

L'etude des Cécidomyies parasites des céréales (celle du blé et celle de l'avoine qu'il réussit a distinguer spécifiquement) le conduit à celle de leurs hyperparasites hyménoptères, en particulier des *Platygaster* et presque immédiatement (1898) à la découverte capitale de la polyembryonie chez *Eucyrtus fuscicollis* (il est juste de rappeler que le premier exemple de polyembryonie avait été signalé en 1894 par S. F. Harmer chez les Bryozoaires Cyclostomes), parasite des Hyponomeutes du fusain, et chez *Polygnotus minutus* parasite de la cécidomyie du blè. On ne saurait trop recommander la lecture du mémoire (1904) in extenso, que Marchal a publié sur cette question. La limpidité, l'élégance de la forme, la netteté parfaite des résultats et surtout la mise en oeuvre méthodique de l'expérimentation méritent d'en faire un des classiques de la littérature zoologique. Je me souviens de l'admiration que m'en manifestait, à Naples, en 1906, Anton Dohrn. On remarquera tout particulièrement le souci constant, chez Marchal, d'expliquer les faits par un déterminisme expérimental précis, ramené à l'action combinée de facteurs concrets bien définis. Marchal est incontestablement un des maîtres de l'expérimentation biologique, qu'il a su manier dans des problèmes particulièrement difficiles.

Au mémoire précédent sur la polyembryonie il faut joindre celui sur les *Platygaster* (1906), où il a mis en évidence les rapports si remarquables de l'hôte et du parasite (kystes à cellules géantes, paranucléus et trophamnios du parasite) et aussi l'un de ses derniers travaux, publié en 1936, sur les Trichogrammes (de la famille des Chalcididés) fruit de dix années de recherches. Il y a montré que le cycle évolutif de ce parasite qui, dans la nature, comporte une alternance regulière de deux générations au cours de l'année, peut être profondément modifié et presenter sept ou huit générations, si on le fait pondre dans les oeufs de Lépidoptères polyvoltins, tels que la noctuelle du chou (*Mamestra brassicae*).

Il a apporté aussi, en diverses circonstances, des contributions d'un grand interêt au problème général de l'espèce, notamment dans ses recherches sur les Cécidomyes, dans celles sur la cochenille du robinier, qu'il a montré être une variété adaptive du *Lecanium corni*, dans celles sur les Chermes (importantes pour les rapports de la reproduction parthénogénétique et de la reproduction bisexuée, 1915), dans celle sur les pucerons, en particulier sur le puceron lanigère (1928).

Etudiant des problèmes qui lui étaient désignés par les nécessités de l'agriculture, il savait en tirer des résultats du plus haut intéret pour la biologie générale.

La maîtrise de Marchal avait été très rapidement reconnue dans le domaine de l'entomologie appliquée et cela lui avait valu notamment, dès 1911, d'être invité par L. O. Howard, à venir étudier aux Etats-Unis, l'organisation du *U.S. Bureau of Entomology* et des laboratoires créés dans les Universités et en dehors d'elles, pour la lutte contre les insectes nuisibles. Ce voyage a fait l'objet d'un magnifique rapport (1916), où l'on retrouve ses qualités eminentes.

Citons encore, parmi ses publications, l'étude qu'il a consacré à la physiologie des insectes dans le Dictionnaire de Physiologie de Ch. Richet (1910). Je signalerai aussi la belle lecture qu'il avait faite à l'Institut de France dans une des séances publiques annuelles, sur L'homme et l'Insecte (1926).

Ces quelques aperçus très sommaires suffisent à donner une idée de l'ampleur, de la varieté et de la valeur exceptionelle de l'oeuvre de P. Marchal, qui conserve une haute efficacité inspiratrice et qu'on ne saurait trop recommander aux jeunes biologistes de méditer. L'homme est inséparable de l'oeuvre. Ce qui caractérisait avant tout Marchal, c'etait sa discrétion, sa modestie allant jusqu'à la timidité. Ces qualités etaient poussées chez lui à un point où elles devenaient presque des défauts, parcequ'elles constituaient un obstacle a l'influence directe qu'il aurait pu et même dû exercer sur les jeunes biologistes. Il ne cherchait nullement à rayonner. Il vivait confiné dans ses recherches personelles, je serais tenté de dire dans son rêve. Mais celui-ci était parfaitement

conscient et méthodique. Il s'était de bonne heure installé à la campagne dans les environs de Paris, à Antony, où il disposait d'une grand jardin outillé pour l'exécution de ses expériences et pourvu, suivant les circonstances, des installations et des plantations nécessaires. Il y vivait en solitaire dans le milieu familial et ainsi il n'a malheureusement pas formé d'elèves. Sa vie etait complétement identifiée à son oeuvre.

J'évoquerai en terminant, une circonstance que je ne connais que par oui-dire, mais que puis donner comme parfaitement authentique. Le carrière de P. Marchal a failli être anéantie avant de commencer. Pendant un de ses premiers séjours à la Station Zoologique de Roscoff, lorsqu'il préparait sa thèse sur les Crustacés décapodes, à un retour de l'île de Batz, l'embarcation où il se trouvait chavira, et il se serait noyé s'il n'avait pas été sauvé par son ainé et maître Georges Pruvot, qui, en cette occasion, n'a pas seulement rempli noblement son devoir humain, mais a rendu une inestimable service à la science. [Je signale une analyse tendue de l'oeuvre scientifique de P. Marchal écrite par P. Vayssière (*Ann. Instit. Agronom.*, **33,** 1942) et celle que le même auteur a publié (*Ann. Soc. Entomol. de France*, **111**, 1942), accompagnée d'un portrait et de la liste complète de ses publications.] MAURICE CAULLERY.

Sir **Frederick William Moore**. Under the two Moores, father and son, the Royal (now National) Botanic Garden at Glasnevin attained a high place in the world of horticulture. David Moore, appointed Keeper in 1838, was succeeded in 1879 by his son. By his recent death at the age of ninety-two, one feels that an epoch in the history of Irish horticulture has closed. The garden was founded, like several other cultural institutions, by the Royal Dublin Society in 1794, and was taken over by the government in 1877 under the Science and Art Museum Act. Under the elder Moore, who was both an experienced horticulturist and an energetic field botanist, the collections were added to greatly, and Glasnevin became one of the leading horticultural centres in the British Isles. Sir Frederick, familiar with the place since childhood, was trained as a horticulturalist, studying and working in Holland, Belgium and Ireland, and was a suitable and worthy successor to his father.

Full of health and energy, he devoted throughout his long life his talents and increasing knowledge to the improvement and extension of Glasnevin ; he was never tempted to stray far from the straightforward task to which he had been called. He did not undertake foreign travel or exploration in search of new or rare plants. A vigorous and emphatic speaker, his voice was seldom heard in lecture-rooms save when he gave courses of instruction to the Glasnevin students ; and as he himself expressed it, he had no time for writing—which is to be regretted, for his knowledge of plants and their culture was very wide and very practical. Independent in mind, and a doughty champion, he fought many a bureaucratic battle for the independence of the Gardens and its importance as a scientific institution ; and he was successful in maintaining their integrity during changing times. Systematic botany he left to the systematist ; I do not think he ever described a new species in his life, though a good deal of undescribed material passed through his hands. He was generous in his distribution of rare plants to those who were qualified to ensure their health, and he recognized the climatic and edaphic restrictions of Glasnevin by placing specimens in gardens especially favoured by nature.

He found time to play his part in the work of local scientific societies ; for many years he was secretary, and later president, of the Royal Horticultural Society of Ireland ; and he had long service on the councils of the Royal Dublin Society, the Royal Irish Academy, the Royal Zoological Society of Ireland (of all of which he was a vice-president). He received the M.A. degree from the Royal University of Ireland, Sc.D., from Dublin University ; he was awarded by the Royal Horticultural Society its Victoria Medal of Honour and its Veitch

Memorial Medal in gold and in silver; and he was one of the first recipients of the Gold Medal of Honour of the Royal Horticultural Society of Ireland. Knighthood for his services to horticulture came to him in 1911.

He leaves a widow (herself a skilled horticulturist), and one son.

R. LLOYD PRAEGER.

Among the many amateur microscopists who have made notable contributions to biological science the name of Mr. **David Joseph Scourfield**, who died on 3 October 1949, will take a high place. He was a clerical officer at the Royal Mint for forty-two years, and his efficiency in this department was recognized when he was made a member of the Imperial Service Order in 1924, two years before his retirement. He was born at Bow in 1866 and lived in the borough until his retirement when he removed to Leytonstone. He was married in 1910 to Miss Julia E. Hills, who survives him.

He was early interested in Natural History, for he became a member of the Bromley Naturalists' Society while still a schoolboy. His main interest was in ' pond life ', particularly the smaller Crustacea, and most of his published papers (over eighty in number) deal with these, although he also made noteworthy contributions to the study of freshwater Protozoa and Protophyta. His work on the Copepoda, Ostracoda and Cladocera made him a leading authority on the systematics of these groups and he made many important observations on various aspects of their ecology. He was especially successful in discovering unusual habitats for them and other microscopic organisms—hollows in tree-trunks, bomb-craters in Epping Forest, the ' leaf-carpet ' of woods, and so forth.

His most important contribution to science, however, was in a different field. His attention was directed to palaeontology when he was asked to identify some fragmentary remains of Crustacea which had been observed in sections of the Old Red Sandstone chert of Rhynie, Aberdeenshire, famous for its marvellously preserved plant remains. These Crustacea are minute, by no means numerous, and are exceedingly fragmentary, although the finest details of structure are visible. The process of grinding thin sections of the rock is very laborious and takes time and the chance of any crustacean fragments being found in a section is small. Scourfield, therefore, hit upon the device of chipping off thin flakes of the chert and examining them in cedar oil or clove oil under the microscope. With indefatigable industry he examined several thousands of such chips over a period of years and drew every crustacean fragment that they contained. The fitting together of these drawings into a credible restoration was only possible for one with his minute familiarity with the structure of recent Crustacea. He described the Crustacean, which he named *Lepidocaris rhyniensis*, in a memoir communicated to the Royal Society in 1925 and published in the *Philosophical Transactions* in the following year *. The writer of this notice had the benefit of painstaking demonstrations by Scourfield of all the more critical points of structure and is prepared to vouch for the general accuracy of his restoration, even in such extraordinary and unexpected details as the association of the male claspers with the maxillulae. It is to be noted, however, that on this last point, as Scourfield himself remarks, the evidence ' is not absolutely conclusive '. Several larval stages were discovered ,and in a later paper communicated to our Society (*Proc.*, 1939–40, pt. 3, p. 290, 1940), two more perfect larvae were described. In the latter paper the larval mandibular palp is figured alongside the same organ from the larva of the living Fairy Shrimp (*Chirocephalus*). The identity of the two organs, even in the arrangement and shape of the bristles with which they are provided, despite the vast period of time that separates them, suggests caution in attempts to estimate the rate at which evolution proceeds.

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* ' On a new type of crustacean from the Old Red Sandstone (Rhynie Chert Bed, Aberdeenshire)—*Lepidocaris rhyniensis*, gen. et spec. nov.' (Pp. 153–187, pls. 21–23.)

In searching for the crustacean remains, Scourfield detected a nearly complete specimen of the oldest known fossil insect, *Rhyniella praecursor* Hirst and Maulik, of which only the head was previously known, and he was able to confirm not only its insectan nature but also its reference to the Collembola suggested by Tillyard.

Scourfield's success with the Rhynie chert fossils led to his being asked to examine a problematical organism (not microscopic) from the Upper Silurian of Lanarkshire which had been conjecturally referred to the Crustacea. With his accustomed industry he collated the evidence given by the twenty-nine specimens, many of them fragmentary, and produced a restoration of which all the main features were confirmed on more than one specimen. He had little difficulty in showing that the organism, to which he gave the name *Ainiktozoon* (*Proc. Roy. Soc.* B. **121**, p. 533, 1937), was not a Crustacean and probably not an Arthropod at all, but, in spite of the complicated and clearly visible structure it was impossible to place it with certainty in any known phylum of the animal kingdom, and it was largely a conjecture that referred it to the Chordata as a ' lowly type allied to the Urochorda '.

Up to the very end Scourfield was busy with his favourite studies and he left unfinished a monograph on the species of the Cladoceran genus *Daphnia*, to which he had given special attention over many years.

He took an active part in the affairs of several scientific societies. He was elected a member of the Quekett Microscopical Club in 1890 and contributed a large number of papers to its *Journal* (of which he was editor, 1900–1903) during more than half a century. He was Vice-President of the Club for several terms and President from 1922 to 1924. In 1942 he was elected an honorary member. He was elected to the Essex Field Club in 1898 and became its President in 1926–1929. He contributed to its meetings many papers and addresses which were published in the *Essex Naturalist*. The Royal Microscopical Society elected him to its Fellowship in 1900 and he served repeatedly on its Council up to 1947. He was Honorary Secretary from 1916 to 1920 and Vice-President in 1914–1921 and 1938–1945. He gave much time and care to the affairs of the Biological Section, of which he was Secretary from 1912 to 1946. He was also a Fellow of the Zoological Society, to which he was elected in 1907.

Scourfield was elected to the Fellowship of our Society in 1926. He served on the Council from 1935 to 1939 and was a Vice-President from 1938 to 1939. He received the Crisp Medal and Award in 1940. His earliest contribution to our proceedings was a paper on ' Entomostraca and the Surface-film of Water', communicated by Professor L. C. Miall and published in the *Journal* in 1894.

Like many amateur microscopists, Scourfield attained a skill in the manipulation of the instrument that many professional biologists could only regard with envy. He also spared no pains in exploring the literature of his subject. The microscope is no longer so popular a toy for the scientific amateur as it was in the days before the hand-camera and the wireless set. It will be a bad day for British Biology, however, when it ceases to have the services of men like D. J. Scourfield.

W. T. CALMAN.

Filippo Silvestri, who died on 2 June 1949 was an entomologist of international repute. A man of immense energy and powerful physique, with a big voice, he seemed to dominate any meeting, and took a prominent part in international congresses. He was born in Bevagna, Umbria, on 22 June 1873, and by July 1896, had become a doctor of science of the Royal University, Palermo.

His contributions to biological literature, almost all concerning Myriapods and Insects, were numerous, totalling well over four hundred and including such major works as a Compendium of Applied Entomology.

His earlier researches, morphological and taxonomic, chiefly concerned Myriapoda, on which he published over ninety communications, but while he retained interest in this group all his life others attracted his attention quite soon, and it was the Thysanura, or Bristle-tails, which he particularly loved to study and describe, contributing well over one hundred papers to the literature. The relationship between mouth parts of Crustacea, Myriapoda, and the section of Thysanura known as Entognatha, containing, *inter alia*, the Papygidae in which he delighted was the subject of a contribution to the fifth International Congress of Entomology in 1932. In this intensive study he concluded that while the maxillipedes of Chilopods are homologous with the first pair of legs in insects, Chilognaths, and Isopods, the buccal appendages are not homologous, but analogous. The crustacean mandible corresponds to the lost appendage of an intercalary segment in insects, the first maxilla to the mandible of insects. Homologies are rendered difficult because, while Insects and Malacostraca have a common origin, the appendages have sometimes been retained for locomotory purposes, while others have been modified, or even suppressed as has happened with the antennule and intercalary appendage in insects. Silvestri advocated establishing the Entognatha as an order, separate from Thysanura Ectognatha, under the name Diplura. These insects are of especial interest as they are considered to be of the type through which all insects have evolved from the primitive group of Symphyla, sometimes classed under Myriapoda.

Many Thysanura are cavernicolous, and these, with other cavernicolous insects, were the subject of several communications.

Since comparative morphology interested Silvestri he found such anomalous insects as *Grylloblatta* especially worthy of study. The best known species of these rare insects, allied to crickets and cockroaches, wingless, and of primitive type, lives in the Rocky Mountains in stony places at an altitude of about 6500 feet. Silvestri considered that *Grylloblatta* constitutes a distinct group, ranking equally with Cockroaches and Termites, and placed between these orders.

Termites were also studied by Silvestri, who paid particular attention to the many kinds of insects associated with them in their nests: about fifty papers were written on this subject, especially towards his later years, until 1947. The similarly bizarre and highly modified associates of ants also received attention.

One of Silvestri's greatest systematic triumphs was the discovery in 1913 of minute, primitive, insects to which he gave ordinal rank under the name Zoraptera; at the present day, however, they are reduced to a suborder and associated with Book-lice, Psocida, in the order Psocoptera.

Silvestri also wrote upon the Symphyla and Protura, and the Embiidae which in social habits show approach to Termites. In his latter years he turned to Strepsiptera, those highly abnormal and isolated parasites of bees and wasps.

It is obvious from all this that Silvestri was a systematist of great experience, but he is also well known for his researches into the embryology of the minute parasites of the eggs of Lepidoptera (Chalcidoidea); a group that received especial attention from him on account of its economic value.

The phenomenon of Polyembryomy, almost peculiar to these parasitic insects, was first adequately described by Marchal in *Encyrtus*, in 1898–1904. The importance of this discovery was well emphasized by L. O. Howard in 1930, in his History of Applied Entomology.

Silvestri, in 1905–16, in other species of parasites, confirmed and greatly extended Marchal's findings. The egg of *Litomastix*, in the *Plusia* moth host, develops first in the egg, but only completes its development in the last stage of the *Plusia* larva. It does not, in the first cleavage, form a relatively small number of cells which remain together in groups gradually differentiated to organize one individual. Instead, it multiplies in enormous numbers to form an elongated asymmetric cellular body which is constricted by an external membrane derived also from a part of the egg, and by a sort of strangulation is separated into pieces numbering about a thousand which attach themselves to the various internal organs of the *Plusia* larva. Since *Litomastix* may lay several eggs in one host egg, there may develop 3000 parasites from one host !

Silvestri pointed out that in polyembryonal parasites cleavage is always total in the somatic blastomeres. This is not the case in other egg parasites ; there the cleavage is limited to the nuclei and leaves the cytoplasm undivided. In polyembryonal chalcids the whole nucleolus remains in one of the blastomeres of the first or second cleavage ; it is the determinant of the sexual cells which differentiate at this early stage, whereas in monembryonal species differentiation takes place very much later.

This precocity has a strange sequel. During development of the separate embryonal masses there are formed groups including somatic with sexual cells, and groups composed only of the more numerous somatic cells. These latter develop precocious larvae differing in structure from normal larvae, and Silvestri termed them ' Asexual larvae '. They are only recognizable as belonging to the same species of insect as the sexual larvae by following their development.

This research was rewarded by a gold medal from the Società di Quaranta of Rome in 1908. Silvestri had from early days been interested in insect pests and their control, and wrote largely on their morphology and habits.

From the date of his paper on polyembryony in 1905 he was an ardent advocate of the value of these minute Hymenopterous parasites, making contributions to the knowledge of them up to 1937.

He will be remembered, perhaps, longer for his work on the control of pests by their natural enemies than for anything else. The part played in this by Italy has been large and honourable. The first attempt at control had been made in Paris by Boisgiraud, who in 1840 combated the ravages of the Gipsy moth on trees by distributing numbers of the predatory beetle *Calosoma sycophanta*. In 1844 Villa, in Italy, used Carabid and Staphylinid beetles against pests in his garden. Riley, in America, in 1871, first suggested that harmful insects could be checked by placing the larvae or pupae in cages of fine gauze in the infested area ; thus allowing the minute parasites which might emerge to escape, while the larger pests themselves could not.

This method was put into practice by Silvestri against the troublesome Trypetid fly of olives, *Dacus oleae*, which he studied very intensively. He also recommended at an early date the cultivation in olive groves of plants which might support insects also serving as hosts for the same parasites which attack the fruit fly.

In 1873 Riley first suggested the transportation of parasites of a widely distributed pest from one part to another in the infested area, and this process was carried further by the introduction into America of *Apanteles glomeratus*, a useful parasite in Europe of the ' Small White ' butterfly which had become a pest in America. Scale insects, which cause enormous losses to fruit-growers were much studied by Silvestri, and in 1928 he communicated to the fourth International Congress of Entomology a paper on the citrus scales of China.

In 1868 an Australian species (*Icerya purchasi*) had found its way to the fruit-growing area of California, and Koebele was sent to Australia to search for its enemies. The ladybird *Novius cardinalis* was introduced into California, and by 1894 had suppressed the scale-insect. Silvestri imported into Italy from California another species of ladybird to combat a scale on olives. This was only one of many importations by him of various predators and parasites, and he travelled extensively to search for them not only on behalf of Italy, but also for Argentina, where he was for two years, and for the United States, and Hawaii. He visited the Mediterranean areas, Eritrea, West and South Africa, Brazil, Uruguay, Peru, Chile, Mexico, Cuba, and New South Wales.

In 1904 Silvestri was appointed Professor of general and agricultural zoology at the Royal School of Agriculture, Portici, and in 1920, on the retirement of his chief, Berlese, became Director of the school.

There was an acute difference of opinion between these two fine entomologists on the question of the use of one, or more than one, species of parasite for the control of a given pest. Berlese was an advocate of mono-parasitism, contending that when an effective parasite had been established the benefits might be thrown away by the introduction of another enemy to the same host. For Hyperparasitism might develop in which one parasite destroyed another, and predators would eat indifferently healthy and parasitized examples of the pest, thereby destroying the parasite. Silvestri, from the beginning, fiercely combated this objection. He contended that since any parasite in nature rarely has *all* the qualities desired by the economic entomologist, the best results will be obtained from the parasite most nearly approaching the ideal, or from a combination of two or more. The point of saturation of the population of any parasite is lower than that of the host : no two parasites are equally resistant to adverse ecological conditions, so that one may be able to parasitise a number of hosts left untouched by another. In the contest with the olive fruit-fly, in which Silvestri took a leading part, he urged that success is possible by means both of other parasites of the same species which might be found elsewhere and by means of parasites of other species, or even other genera, in other countries. The success of the control of the Zygaenid moth in Fiji, which devastated coconut trees, by means of parasites of another genus of moth from Malaysia, is a striking vindication of this view. This example leads naturally to the consideration of the reverse situation. The ' Small White ' butterfly has been mentioned as destructive of cabbages ; if, however, the cabbage plant should so over-run the garden that nothing else would grow, then the butterfly would be hailed as a saviour.

Silvestri paid attention to this aspect also of control which has of recent years come much to the fore, with some astonishing successes.

He saw the dangers, however, and emphasized that the insect which it is proposed to introduce against a plant pest must be most carefully studied beforehand to make sure that under all conditions, even of starvation, it will not attack anything but the plant pest. As Director of an Agricultural School he very suitably pointed out that complete destruction of all weeds in agricultural land might be harmful rather than beneficial. For weeds are not always an unmitigated nuisance ; they may be traps for injurious insects or serve as a reserve supplying useful parasites.

To a man of such parts as Silvestri honours inevitably came. The award of a gold medal in 1908 has been mentioned ; in 1945 the R. Academia dei Lincei of Rome gave him a Royal Prize for his work, and about 1930 he received the Grande Médaille I. Geoffroy St. Hilaire of the Société National d'Acclimatisation de France and a gold medal from the Istituto fascista di tecnica e propaganda agraria. Many zoological and entomological societies made him a Corresponding Member ; the Foreign Membership of the Linnean Society of London was conferred upon him in May 1933. The American Association of Economic Entomologists made him a Foreign Member, and Honorary Fellowship was conferred upon him by the Royal Entomological Society of London. He was Honorary Correspondent of the Zoological Survey of India, an Honorary Member of the Société Entomologique de France, the Association of Economic Biologists of England and the Real Sociedad Espñaola de Historia Natural. The R. Academia dei Lincei of Rome made him a National Fellow in 1920.

G. D. Hale Carpenter.

Vladímir Leontyèvich Komaróv was born in St. Petersburg (now Leningrad) on 13 October 1869. From early childhood he showed a love of nature, and formed a herbarium while still at school. Although no natural science was taught at the school which he attended, he read books on natural history continually ; and when the time came for entering the university of St. Petersburg, which he did in 1890, he enrolled for physics and mathematics, in the face of considerable family disapproval. Here he studied botany under the botanist-geographer A. N. Beketov, who also numbered among his pupils such well-known figures as K. A. Timiryàzev, A. N. Krasnov and N. I. Kùznetsov. He became greatly absorbed in Darwinism, and even translated the entire *Origin of Species* into Russian, though he subsequently, ' in a moment of severe self-criticism ', burnt the manuscript. At about this time, too, the teachings of Marx and Engels began to attract him, and subsequently claimed his enthusiastic adherence. In 1892 and 1893, while still at the university, he undertook extensive journeys in the upper course of the Zeravshan River in Central Asia, and was deeply impressed by the immense part played by glacial action in this typical high-mountain glacier country. Thence he penetrated the Kara-Kum desert, a region forming an extreme contrast to the Zeravshan valley, though lying so close to it, and this led him to profound reflections on the role of natural factors in the origin and distribution of plant-species and communities.

Upon graduating, he managed after some difficulties to attach himself to the Amur Railway Survey (he was exempted from military service owing to poor health), and set out by sea for Vladivostók in 1895. The Trans-Siberian Railway was not then completed. This was the beginning of his systematic researches in far eastern Asia. With Khabarovsk as his summer headquarters, he made extensive collections and investigations of the flora of the Amur region, in the winter returning to Blagoveshchénsk to work up the results. One important result of this expedition was the economic development and settlement of the region, on Komarov's recommendation. For Komarov was never a ' pure ' scientist : he was always eager to relate the results of scientific discovery to the needs of mankind, and of his country in particular. This outlook characterized his whole life, and, combined as it was with great vivacity and personal charm, makes it easy to understand the great regard in which he was held by his countrymen.

From Amuria, Komarov turned his attention to Manchuria, to the south. In 1896 he undertook a journey through the whole of Central Manchuria, and this was followed during the next two years by the organization of a still larger-scale expedition to southern Manchuria and northern Korea, under the auspices of the Russian Geographical Society.

The outcome of this series of explorations was the appearance of the first instalment of Komarov's great *Flora of Manchuria* in 1901. This formed his thesis for the degree of Master of Botany. It was a work of high quality, and led to the award of the Przhevalsky medal from the Geographical Society, the Baer prize from the Academy of Sciences, and a special medal with portraits of Tournefort and Linnaeus from the International Academy of Botanical Geography.

In 1902 Komarov set out again, this time for Eastern Siberia. He went south from Irkutsk and Lake Baikal into Northern Mongolia, penetrating up the Irkut River to the highest peaks of the Sayan Range. This range he crossed, made a circuit of Lake Kosogòl, and returned to Irkutsk. His account of this journey has been described as a classic of geographical research. He grasped the significance of the geological features of the region, particularly in relation to its glacial history, and in the light of this presented a correspondingly able account of the vegetation.

In the years following this expedition, Komarov spent some time working at the university. Here he met Nadezhda Viktorovna Stark, who afterwards became his devoted wife and faithful companion and fellow-worker. During this period he visited France and England, and worked for a time at the Royal Botanic Gardens, Kew.

With the year 1908, there opened yet another phase in Komarov's investigations of the flora of the Far East. He commenced the exploration of the almost unknown land of Kamchatka, which even as late as the closing-years of the nineteenth century was, for practical purposes, in the words of the geographer Shokalsky, ' on another planet '. During 1908–1909 he covered the greater part of the southern half of the peninsula, and once again presented the results in a masterly volume dealing with the geography, geology, topography, plant and animal life, and economic possibilities of the region. His *Flora Poluostrova Kamchatki*, embodying his own and earlier botanical work on Kamchatka, was ready for the press in 1916, but did not actually appear till 1927–30.

In 1912 Komarov published an important work entitled *Contributions to the Flora of China and Mongolia*, which formed the thesis for his doctorate. In 1913 he was commissioned by the Resettlement (Colonization) Administration to undertake a journey in the Southern Ussurian region, during which he travelled from Vladivostók to Lake Hanka and over much of the adjoining territory. The botanical results of this expedition were embodied in his *Types of vegetation of the Southern Ussurian region.*

In 1914 Komarov was elected a Corresponding Member, and in 1920 a regular member, of the Academy of Sciences, and he retained a highly distinguished and increasingly close connection with that body to the end of his life, becoming Vice-President in 1930 and President in 1936. In 1918 he accepted the chair of botany in the University of Petrograd—he termed it the ' chair of plant-morphology and ecology '—and in the course of the twenties founded the great school of botany at the Academy of Sciences. He regarded university teaching as inseparable from his scientific activity ; hence the text-books that he published were often classical scientific monographs, while conversely many of his purely scientific works came to be widely used as text-books. In all this he had the active help of Mme. Komarova-Stark, and she was jointly responsible with him for such works as his *Structure of plants*, *Types of plants*, and *Origin of plants*. In a later book, on *The study of the Species in Plants* (1944), he summarized his views on the more theoretical side of botany, which had always interested him.

In 1926 Komarov headed the Soviet delegation to the Third Pacific Science Congress, held at Tokio, and contributed a short paper ' On the Arctic Limits of some Trees of the Russian Far East '. Subsequently he became interested in the territory of Yakutia in north-east Siberia. Between 1930 and 1935 he undertook a further expedition to the Far Eastern Region, and others to Central Asia and the Caucasus. Towards the close of the thirties he directed his attention to the flora of the Riviera and of the Chamonix valley in Switzerland. But perhaps the crowning scientific achievement of his later years was the launching of the great *Flora of the U.S.S.R.*, the first volume of which appeared in 1931 and the most recent, the fifteenth, in 1949.

It was natural that Komarov's intense patriotism should find many opportunities for expression during the late war. One such opportunity was provided by the appointment in 1941 of the Komarov Commission to secure the mobilization of the resources of the Urals, and subsequently those of Western Siberia and Kazakhstan, for the needs of defence. His genius for organization and his ardent public-spiritedness, undimmed by advancing years (he was then seventy-two), stood his country in good stead at this critical time, and under his energetic leadership the Commission worked out new methods of collective activity and production which probably had far-reaching results.

He was elected a Foreign Member of the Linnean Society of London on 7 June 1945, and in the same year the Academy of Sciences of the U.S.S.R.

published a large volume (over 700 pages) of selected extracts from his writings, including a biographical sketch from which many of the foregoing details are taken.

V. L. Komarov was a man of outstanding character and ability. It is a matter for regret that, owing to the language difficulty, much of his work necessarily remains unknown to many outside his own country. But for breadth of outlook, energy, industry, and record of solid achievement, there can be little doubt that he must be ranked among the great figures of botanical science.

H. K. AIRY SHAW.

Albert Wilson (1862–1949) was born at Calder Mount, near Garstang, Lancashire, on the 12 October 1862, and died at his home in Priest Hutton, near Carnforth on the 15 May 1949, after a long illness, leaving one son. He was educated at Quaker schools in Kendal and Hitchin, and there developed the keen interest in field botany and love of the countryside which were to result in the production of two major works on county flora during his lifetime. Upon leaving school he was apprenticed to a firm of Pharmaceutical Chemists in Bradford, and, after passing the examinations of the Pharmaceutical Society, ultimately became a partner in the firm. In 1890 he married Alice Mary Thorp, and in his fiftieth year retired from business.

Mr. Wilson was elected a Fellow of the Linnean Society in 1900, and also became a Fellow of the Royal Meteorological Society, contributing meteorological and phenological notes regularly to the *North Western Naturalist*. His botanical interests were wide, embracing flowering plants, bryophytes and lichens, and he was one of the earliest members of the Moss Exchange Club (later British Bryological Society), compiling the third edition of the *Census Catalogue of British Hepatics* for the Society in 1930. He was also an active member of the Botanical Society and Exchange Club, contributing records and beautifully prepared material over a long period of years.

In 1893 he made the acquaintance of John Alfred Wheldon, of Liverpool, thus beginning a close friendship and collaboration which lasted until the death of Wheldon in 1924. In 1907 they published the *Flora of West Lancashire*, a work on the flowering plants and cryptograms of vc. 60 which, with its pronounced ecological outlook and detailed critical work marked a new era in county floras. Both authors had a profound knowledge of bryophytes and lichens, and after the publication of this work extended their cryptogamic researches to parts of the Scottish Highlands. In the *Journal of Botany* (1908, 1910) they published a paper on the Inverness Cryptogams, giving a systematic list and an ecological analysis of some lichen associations. This was followed by a paper on the Lichens of Perthshire (*Journ. Bot.*, 1914, 1915, Suppl.).

The vertical range of plants was a subject of great interest to Albert Wilson, and in 1931 he published a valuable paper on ‘ The Altitudinal Range of British Plants ’ in the *North Western Naturalist*, with a Supplement in 1940. In 1932 he decided to write the *Flora of Westmorland*, and it says much for his intellectual vigour and immense capacity for work that he could carry through such an undertaking so successfully at this time. The Flora, again including bryophytes and lichens, was published in 1938, when the author was seventy-six years of age, and is a worthy companion to the *Flora of West Lancashire*, embodying years of field work in the county. The delightful photograph of the author at work, one feels, was only reluctantly admitted, as it appears at the end of the book, and is not even included in the index. Of a shy and retiring disposition, his advice and help were always most willingly given in botanical matters, and his clear, firm handwriting was at once a joy to read and a guide to his character.

His last published work was on ‘ The Flora of a Portion of North-East Caernarvonshire ’ (*N.W.Nat.*, 1946, 1947), containing many interesting records, and valuable cryptogamic work.

In 1946 he gave his extensive herbarium, consisting of more than eight thousand specimens of British flowering plants, bryophytes and lichens to the Yorkshire Museum, York. C. W. MUIRHEAD.

Frederick William Mills was born on 26 March 1868, at Huddersfield, Yorkshire, and was educated at Rugby School. On leaving there he studied law and went into the family business as a solicitor. This career he entered unwillingly at the insistence of his father, for he himself wished to join the medical profession. He found, however, that a legal practice, particularly on the commercial side, offered great scope to one of ability and energy, and he built up one of the largest and most successful in the North of England. He retired in 1922, by which time he was beginning to find the work very heavy going. He then left Huddersfield and went to live in Devon. He died on 5 October 1949, at his home at Monkleigh, near Bideford.

Mills never allowed himself to become completely preoccupied with his profession, and among his chief interests were photography and microscopy. Whilst still in his teens he won the Premier Award at the Vienna International Exhibition of Photography. Combining these two interests he published a small book, *Photography applied to the Microscope*, in 1891 at a time when the subject was still in its infancy. This was a most useful treatment for the amateur worker and was very well received.

Mills' chief microscopical interests were the Foraminifera and the Diatomaceae, especially the latter. Of these he wrote a good introductory account which, together with a most comprehensive bibliography of the group prepared by Julien Deby, was published in 1893 as a book under the title of *An Introduction to the Study of the Diatomaceae*. Shortly afterwards he collaborated with R. H. Philip in an important paper on *The Diatomaceae of the Hull District* which was published in the Transactions of the Hull Scientific and Field Naturalists' Club in 1901. The text consists of a list of specific names and localities, but it is accompanied by seventeen plates in which all the species listed are figured. This was the first comprehensive series of illustrations of British Diatoms available at a reasonable price since W. Smith's *Synopsis of the British Diatomaceae* published 1853–6, and the paper was accordingly much sought after.

During the following thirty years Mills published a few small papers on the Diatomaceae and Foraminifera. He was elected a Fellow of the Linnean Society in 1918. He published his comprehensive *Index to the Genera and Species of the Diatomaceae and their Synonyms*, issued in 21 parts in 1933–5. This was produced by a duplicating process, and not by printing, which did not allow corrections to be made so readily in proof, and accordingly errors are rather numerous. This has to be borne in mind when using the work, but it is nevertheless an indispensable tool for any worker on the group. It contains over 500,000 references to more than 60,000 specific and varietal names. The foundation of the work was Peragallo's *Catalogue Générale des Diatomées*, 1897, and this goes back, through other such catalogues, to that produced by Habirshaw in American in 1878, of which fifty copies were made by the ' Electric Pen ' for presentation to the author's friends and correspondents. A few miscitations can be traced through the whole series of these works from Habirshaw to Mills. Mills originally compiled this great Index for his personal use and was persuaded with difficulty to make it generally available.

Mills never mounted any microscope slides himself, but he amassed a collection of several thousand, mostly by purchase. The Diatoms formed the greater part of these, but he parted with them about 1930 to the late F. W. Adams, an extremely rich collector and amateur student of the group. They are now in the British Museum (Natural History). The sale of these slides to Adams had its amusing side. Adams had been worrying Mills to sell the collection to him for a long time. Mills, getting tired of this, wrote to Adams offering him the collection for a price of £500, which he regarded as so fantastically high that it would stop Adams for good. The next morning Adams arrived with a cheque and a van.

Mills had a remarkable photographic memory, and acquired an encyclopaedic knowledge of Diatom literature. This enabled him to refer at once to any published illustration or record when naming a specimen. This knowledge was freely placed at the disposal of any student of the group, and he was always ready to lend rare books and papers in his possession to other workers. He was always most helpful and encouraging to beginners who approached him for advice and assistance, and his loss will be severely felt by all diatomists who were his correspondents. R. Ross.

Dr. **Robert Gurney**, who contributed so much to our knowledge of the Crustacea, died at Oxford on 5 March at the age of seventy. Zoology has lost a devoted worker who took infinite pains to make our knowledge of the groups he chose to study as exact as possible ; his monographs and many papers on both the freshwater Copepoda and the larvae of the Decapoda are models of zoological scholarship at its best. He was also a field naturalist with a love of nature in all its aspects.

The fourth son of John Gurney of Sprowston Hall, Norfolk, he was born in 1879. From Eton he came up to Oxford as a scholar of New College and in 1902 graduated with First Class Honours in Zoology. He seems to have been attracted to the Crustacea from the very beginning of his zoological studies ; his first paper, which was published in the *Quarterly Journal of Microscopical Science* in 1902, was on the metamorphosis of *Corystes cassivelaunus* (Pennant) and was sent to press while he was still an undergraduate. Two more papers on the development of decapods appeared in 1903 and in the following year came his first paper dealing with the freshwater Copepoda. So began the long series of papers on these two groups, the Decapoda and the Copepoda which he was to continue for nearly half a century to the time of his death. He was attracted equally to the study of life in freshwater and in the sea. His first paper, like a number of others, was based upon material he had collected himself in tow-nets when working from the Plymouth laboratory. He seems at once to have realized the need for a laboratory specially situated to promote the study of freshwater biology just as Plymouth and Naples were advancing our marine knowledge ; he and his brother Eustace together founded the first freshwater laboratory in Great Britain at Sutton Broad only a year or two after he left Oxford. In this he was before his time—his pioneering effort unfortunately did not receive the support he had hoped for and it did not survive the first world war ; the number of freshwater biologists in the country then was very small. It was not until many years later that, with his active support, the Freshwater Biological Association was formed and the flourishing laboratory on Lake Windermere came into being.

While most of his freshwater work dealt with the Copepoda, in 1909 he published a general account of the freshwater Crustacea of Algeria and Tunisia as a result of a special collecting expedition he made in the spring of 1906. Here he discovered and described a very interesting new species of subterranean isopod *Cirolana fontis* whose nearest relatives are marine and live below the shore line of the Mediterranean. In a separate account of this species (*Zool. Anzeig. 32*, 1908, p. 682) he discussed the possibility that such subterranean crustacea may be derived not, from the surface, but directly from the lower layers of the sea itself by means of the outflows of subterranean waters which connect with the sea at deeper levels. He supported this very interesting suggestion with other examples of close relationship between subterranean and marine crustacea. On this same short expedition he also discovered six other new crustacea : an anostracan, a cladoceran and four species of copepod.

The crowning achievement of his freshwater work was his important three volume monograph of the British Freshwater Copepoda published by the Ray Society between 1931 and 1933. Here he described fully, and illustrated with his beautiful black and white drawings, all the British species; he gave not only all the details of their adult anatomy, but their development wherever known and a discussion of their distribution and bionomics. As well as the many papers on British species he also wrote a number on collections of Copepoda sent to him from different parts of the world.

In his work on the marine Decapod larvae his plan of campaign followed the same pattern: a very long series of papers, some of which were large expedition reports and then a drawing together of his results in two further Ray Society volumes. First came the complete Bibliography of the group in 1939, to be followed by the monograph proper 'Larvae of Decapod Crustacea' which appeared in 1942; in these two volumes he gathered up the fruits of nearly forty years' study. In addition to much work in home waters he had made several journeys abroad to investigate the fauna of specially interesting regions and had also examined and reported on the more important collections made by marine expeditions leaving this country to explore the different oceans: for example the *Terra Nova* and the Great Barrier Reef Expeditions, and the long series of voyages of the Royal Research Ships *Discovery* and *Discovery II*. He was a member of the Cambridge expedition to the Suez Canal in 1924 and twelve years later returned again to that region to work at the marine station founded by the late Dr. Cyril Crossland at Ghardaqa on the Red Sea. In 1935 he visited Bermuda with his brother-in-law the late Professor Walter Garstang, and there for the first time became acquainted with living specimens of the larvae of the deeper water crustacea in which he had become so interested by examining the material brought back by oceanic expeditions. Bermuda, a laboratory sitting on a pinnacle arising abruptly from deep water, is almost like a research ship anchored in mid ocean; it was a great experience for them both, and he and Garstang returned together for a second visit and rich harvest of material in 1938.

Gurney never held any official zoological position; all his life he worked in his own private laboratory at home, at first in Norfolk and latterly on Boars Hill above Oxford. Because of his modest and retiring nature, and because he worked privately, the extent of his zoological achievement was not perhaps as well known as it should have been; but all those who came across his work were full of admiration at its quality and he was awarded his Oxford D.Sc. in 1929 before any of his larger monographs had appeared. I will now quote from a letter I received from our former President, Dr. W. T. Calman, C.B., F.R.S., after Gurney's death, because I am sure what he says is very true: 'His frequent silence as to the wider implications of the facts he was recording by no means indicated that he did not recognize these implications. It was only his diffidence that led him to abstain from discussing questions that others might be better qualified to deal with'.

The comparison he drew between the Protozoea stage of the decapod larvae and the Copepoda was, as Dr. Calman wrote further in his letter, 'one of Gurney's most promising suggestions'. His reluctance to speculate and the modesty with which he put forward what was a most exciting new idea in phylogeny is illustrated very well in his discussion of this comparison in his monograph: 'Larvae of Decapod Crustacea', pp. 22–26. He began by saying 'Something should be said here of a possible relation between the Decapoda and the Copepoda', and then he gave a detailed comparative study which most zoologists would regard, I think, as evidence of very considerable weight and which one feels has really convinced him; he ended this brilliant argument, however, thus: 'While it must be admitted that evidence of this kind is not very substantial, it does justify putting forward the speculation that the

Copepoda have arisen by arrested development from a larval form having the general characters of the Decapod Protozoea '. It is indeed remarkable, not to say romantic, that in early life he should have singled out from all the many groups of Crustacea these two, the Copepoda and the Decapoda, to be the objects of his life research ; and then, only towards the end of his work, that he should come to find that the evidence, which he had been so carefully collecting, was pointing to the conclusion that these two groups, hitherto regarded as so widely separated and at first sight so fundamentally different, are in fact perhaps the most closely related of all the Crustacean orders. Calman, in 1909, in his Crustacean volume of Lankester's *Treatise on Zoology* (p. 26), when discussing cephalic appendages, wrote ' It is possible, however, that in these characters the Copepoda are persistently larval rather than phylogenetically primitive. . . ' Thirty years later Gurney was to show that the Copepoda most likely carry the larval characters of the Decapods ; that in fact the most successful or abundant group of arthropods in the sea has arisen by an evolutionary process of paedomorphosis from the larvae of another group, just as, curiously enough, the most successful arthropods of the land, the insects, appear to be similarly derived from larval myriapods. If fully established, Gurney's modest speculation is a discovery in comparative anatomy of great evolutionary significance.

Gurney's views on larval forms were no doubt developed under the influence of frequent discussions with Garstang. He showed clearly how the commonly held view that the larval forms of to-day represent, in a modified form, ancestral adult stages can no longer be upheld. Like Garstang and de Beer he provided much ammunition for the demolition of Haeckel's so-called, and once most fashionable, ' biogenetic law '. Gurney and Garstang together wrote a very suggestive essay on ' The Descent of Crustacea from Trilobites ' in the volume, *Evolution : Essays on Aspects of Evolutionary Biology*, presented to Professor E. S. Goodrich on his seventieth birthday (1938). On page 277 they wrote : ' Summing up, we conclude that Crustacea were not derived directly from Annelids, or along with Trilobites from a common Annelid ancestor, but from Trilobites themselves as two distinct strains (diphyletic). Branchiopoda arose from typical anomomeristic Mesonacida of the Lower Cambrian, and Phyllocarida almost certainly from the later Olenelline branch, in which the body had already acquired the fixed number of 14 trunk somites, together with an incomplete 15th somite, devoid of pleura, but carrying a terminal dorsal spine. The origin of typical Malacostraca cannot be far removed from that of Phyllocarida, but needs an ampler consideration of the whole life-history than we can enter upon within the limits of this essay.'

Later, in discussing Crustacean development in his 1942 monograph, Gurney pointed out that in no Branchiopod is there any marked metamorphosis, whereas in the Copepoda, Ostracoda, Cirripedia and Decapoda, that is to say in all other Crustacea which have free larvae, there is. ' It may well be ' he said, ' that this distinction corresponds to a fundamental cleavage in the Order ' and he referred in a footnote to the passage in the essay with Garstang just quoted.

Gurney, by his long and patient researches has presented zoologists with a mine of solid facts. Beyond the very significant suggestions, to which I have referred, he refrained from elaborating phylogenetic theories ; to quote Dr. Calman again ' only his diffidence in putting forward any views that might be regarded as " speculative " prevented him from anticipating conclusions that will doubtless be drawn by others from his data '.* Let us hope that Gurney's foundations will always be remembered when others build upon them.

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* Obituary notice in *Nature*, *165*, 587.

He was a man of great personal charm, but, particularly in his early years, shy and retiring. He could never bear to be idle ; always he felt that he must be occupying his time with something useful. The ruling passion of his life was service to the community ; first by adding to human knowledge, and secondly by helping to lead the younger generation towards a better sense of citizenship. It was this second urge which made him have his keen interest in the Boy Scout movement in which he and Mrs. Gurney took such an active part. There can be no better comment on his work in this field than the following quotation from the letter of a Norfolk friend : ‘ One sees down here how many lives he has influenced for good, how many boys, now men, have learnt to see things in a better way and to love the country.’

His native county, Norfolk, owes much to his generosity both in time and money ; he had a great deal to do with the reorganization of the natural history collections and exhibits in the Norwich Castle Museum, and for many years was chairman of the Norfolk and Norwich Hospital. His wide interest in natural history is shown by the excellent articles for the general reader which he contributed in recent years to *The Illustrated London News* and in his delightful little book, which he illustrated with his own drawings, on *Our Trees and Woodlands.*

A. C. HARDY.